Cranial anatomy and phylogeny of the South-East Asian catfish genus *Belodontichthys*

G. J. HOWES

Department of Zoology, The Natural History Museum, London SW7 5BD England

AYANOMIYA FUMIHITO

*Department of Zoology, University of Oxford, Parks Road, Oxford OX1 England

CONTENTS

SYNOPSIS. The cranial anatomy of the south east Asian silurid catfish *Belodontichthys dinema* (Bleeker, 1851) is described. Comparison is made with other members of the Siluridae and a suite of synapomorphies identified. From these it is inferred that *Belodontichthys* is the sister-group to *Ompok bimaculatus* and they, in turn, form the sister-group to *Wallago*. The genera 'Ompok' and 'Kryptopterus' are recognised as non-monophyletic assemblages. Neurocranial features of *Belodontichthys* are examined in the context of their function and hypothesised evolutionary development.

INTRODUCTION

The genus *Belodontichthys* was proposed by Bleeker (1858) in his revision of siluroid fishes. The genus consisted of the type species (*dinema*) which he had previously described as a member of the genus *Wallago* (Bleeker, 1851). Bleeker's specimens were from Borneo; since then the species has been recorded from Sumatra, Java, Laos, Vietnam, Thailand, Kampuchea and Malaysia (Haig, 1950; Kottelat, 1985, 1989; Roberts, 1989). The genus is currently recognised as monotypic and assigned to the family Siluridae.

Even for a siluroid *Belodontichthys* has an extraordinary external morphology (Fig. 1A). The fish is elongate, strongly compressed with a long anal fin (85–97 rays), short dorsal fin (4 or 5 rays) and a small but deeply forked caudal fin. The pelvin fins (9 or 10 rays) are minute but the pectoral fin (18–21 rays) is elongate and wing-like, extending to beyond the anal fin origin. The head is narrow with a straight to concave dorsal profile (formed by the anteriorly extended dorsal body musculature) (Fig. 1B). The eyes are large, set at the corner of the mouth; the jaws long, and obliquely angled, with the lower jaw extending anteriorly beyond the upper (Figs 1B, C); both jaws are armed with three rows of long teeth with arrow-shaped tips. The maxillary barbel extends only to the pelvic fins; and the single pair of mandibular barbels are shorter than the diameter of the eye. Gill-rakers are elongate, numbering *ca* 30.

In spite of its peculiar morphology, the anatomy of *Belodontichthys* has not previously been described. Perhaps this is because it is not abundant in museum collections although relatively common in nature (Haig, 1950). This paper is the result of the collection by one of us (A.F.) of specimens in Thailand which has provided the opportunity for a detailed anatomical investigation. Our study is restricted to the anatomy of the neurocranium, jaws, hyomandibular and palatoquadrate osteology and associated myology. It is hoped, however, that future work by one of us (A.F.) will describe the other skeletal structures. Despite the anatomical limitation of our investigation we believe it has uncovered several previously unknown features which point the way to a more refined phylogenetic analysis of the Siluridae.

The habits of *Belodontichthys* are poorly known. Smith (1945) remarks that the fish occurs in deeper waters and feeds on migratory schools of young cyprinids. We are informed by Mr Chavalit Vidthayanon that the fish usually stays close to the substrate or in the middle of the water column but takes its prey from near the surface. Adults congregate in small groups of 5–10, subadult groupings usually comprise more than 10 individuals. Adults feed primarily on fishes, and juveniles on insects and crustaceans. Eggs are adhesive.

The pelagic and predatory habits of *Belodontichthys* apparently resemble closely those of the schilbeid siluroid *Europiichthys vacha* which according to various accounts

* Present address: Yamashina Institute for Ornithology, 115 Tsutsumine-aza, Kōnoyama, Abíko-shí, Chiba 270–11, Japan.
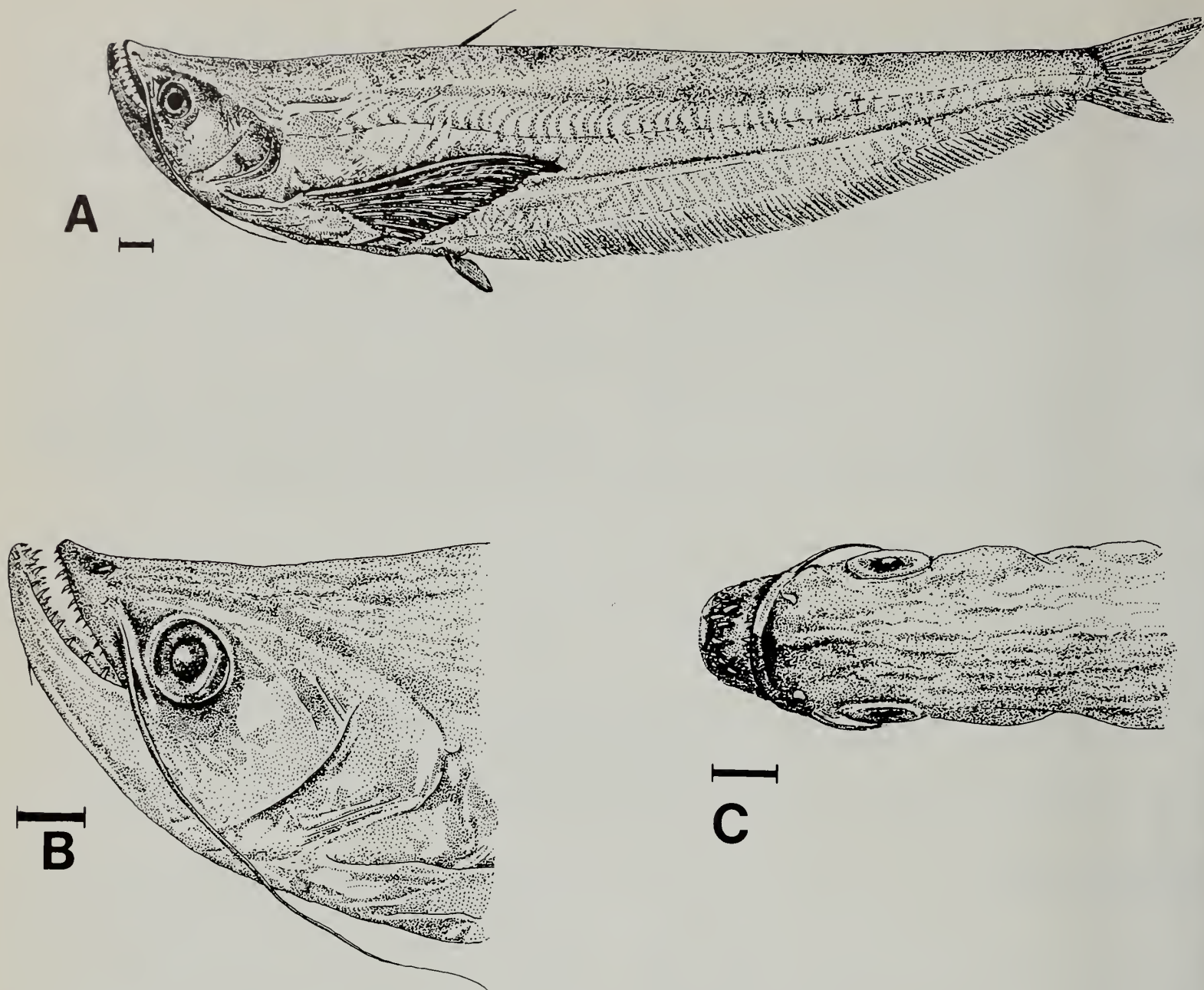
Fig. 1 *Belodontichthys dinema*: A, lateral view of the whole fish; B, lateral view of head; C, dorsal view of head showing overlap of teeth in the upper jaw by those in the lower jaw. Drawn from LILI 89007, 320mm SL. Scale bars = 10mm.

reported by Hora (1937) is also a fast-moving pelagic and voracious fish (see p. 158).

METHODS AND MATERIALS

In making our phylogenetic analysis we have concentrated principally on in-group comparisons to other silurids since our concern has been the immediate relationships of *Belodontichthys*. The monophyly of the family Siluridae has been demonstrated by Bornbusch (1988; 1990) and corroborated by our out-group comparisons with a wide-range of siluroid taxa involving the families Ariidae, Bagridae, Clariidae, Diplomystidae, Ictaluridae, Pangasiidae, Pimelodidae, Plotosidae Schilbeidae and Sisoridae. In making out-group comparisons we have accepted that the Diplomystidae represent the sister-group to all other siluroids and so follow Grande (1987) in recognising a primary division of the Siluriformes into the Diplomystoidei plus Siluroidei.

Although we have also used Grande's (1987) description of the Eocene †Hypsidoridae as a source for comparisons we are less sure that it truly represents the sister-group of all other siluroid families as proposed by Grande since †*Hypsidoris* seems to possess several advanced features shared with some siluroids (T.P. Mo pers. comm.).

NOMENCLATURE: Osteological nomenclature follows that of Patterson (1975). We have adopted the term posttemporo-supracleithrum used by Arratia (1987) since we believe this most satisfactorily describes the structure whose incorporated elements are a matter of debate (Lundberg, 1975; Fink & Fink, 1981; Howes, 1983a; Arratia, 1987). Muscle nomenclature follows that of Winterbottom (1974). Reference to *Ompok* in comparative sections refers to *O. bimaculatus* (particularly specimens from the Sittang River, Myanmar); see p. 155 for further discussion.

LIST OF SPECIMENS USED FOR ANATOMICAL STUDY: (BMNH = Collections of the Natural History Museum, London; IBRP = Research Institute of Evolutionary Biology, Tokyo University of Agriculture; LILI = Ligong Laboratory

of Ichthyology, Tokyo; ZMA = Institute of Taxonomic Zoology, University of Amsterdam). Preparations; CS = cleared and stained; D = dissected; S = dry skeleton):

Aorichthys aor BMNH 1891.11.30:224, Sittang R. Myanmar (S, cranium 65 mm); *Bagarius yarrelli* 1889.8.29:2, Hooghly R., India (S, cranium, 515 mm); *Bagrichthys macracanthus* BMNH Uncat. locality unknown (D, 110 mm SL); *Bagrus bayad* BMNH Uncat., Nile (S, cranium 118 mm); *Belodontichthys dinema* LILI 89008 (D, 343 mm SL, cranium 51.5mm); LILI 89002 (CS, 150 mm SL); LILI 89007 (D, 320 mm SL); LILI 89002 (D, 125.5 mm SL) all Ubonratchauthani, Thailand; IBRP 6625 Singtang market, West Kalimantan, Indonesia. (D, 202mm SL, cranium, 34.5mm); *Chrysichthys cranchii* BMNH 1900.12 Albertville, Tanganyika (S, cranium 118mm); *Eutropiichthys vacha* BMNH 1891.11.30:162–9 (D, 175mm SL), (S, cranium 39mm) both, Sittang river, Myanmar; *Hemisilurus heterorynchus* BMNH 1982.3.29:161–2 Kapuas, Borneo, Indonesia (D, 250mm SL, S, cranium 41.5mm); *Hito taytayensis* 1933.3.11:110–2 Culion, Philippines (D, 148mm SL); *Ictalurus punctatus* 1898.12.29:171 Arkansas (S, cranium 33.5mm); *Kryptopterus amboinensis* 1864.5.15:4 No locality (D, 128mm SL); *K. apogon* LILI 89016 (D, 195mm SL; S, cranium 74mm); LILI 89010 (D, 123mm SL; S, cranium 31mm) both from Moon R., at Khong Chiam, Ubonratchathani, Thailand; *K. bleekeri* LILI 89030 Borapet canal at Bung Borapet Fisheries Station, Nakorn Sawan, Thailand (D, 194mm; 250mm SL; S, cranium 34mm from 149mm SL specimen); *K. bicirrhis* BMNH 1982.3.29:163–7 Kapuas R., Borneo (CS, 58mm SL; D, 60mm SL); *K. cryptopterus* LILI 89009 Borapet Canal (CS, 102mm SL; D, 105, 115 mm SL); BMNH 1982.3.2.168 Kapuas R. (D, 112 mm SL); *K. limpok* BMNH 1980.12.16:18 Vientiane (D, 230 mm SL); 1891.1.27:14 (S, cranium 26 mm); *K. cf. macrophthalmus* BMNH 1905.1.26:5 Borneo (D, 221 mm SL); *K. micronema* BMNH 1892.9.2:25 Simbang R., Borneo (D, 280mm SL); *K. moorei* LILI 89018 Moon R., Haad Saeng Thian, Thailand (D, 155mm SL; D, 161mm SL, and cranium, 24mm); *Mystus nemurus* Lake Bung Borapet, Nakorn Sauan, Thailand (S, cranium 24mm); *Ompok bimaculatus* LILI 85003 (D, 137mm SL), BMNH 1889.2.1:2477–8 (D, 170; cranium, 31.5mm), 1891.11.30:179 (S, cranium 35.5mm) both Sittang R., Burma, 1889.2.1:2499–504 Sind (D, 110mm SL, cranium 18mm); *O. liacanthus* BMNH 1891.1.27:15–27. Kapuas (D, 112mm SL); *O. pabo* BMNH 1891.11.30:180–3 Sittang R. (D, 202mm SL); *Pteropangasius cultratus* LILI 89035 Nakorn Sawan, Thailand (S, cranium 39mm); *Pimelodus maculatus* BMNH 1861.1.19:24 Sao Paulo (S, cranium 49mm); *Plotosus caneus* 1889.2.1:2529 Calcutta (S, cranium 60mm); *Proeutropiichthys taakree* 1891.11.30:199 Sittang (S, cranium 60mm); *Schilbe mystus* 1982.4.13:3242–50 Nigeria (D, 106, 107mm SL); *S. uranoscopus* 1850.7.29 Nile (S, cranium 58mm); *Silurichthys hasseltii* 1970.9.3:178–82 Singapore (D, 83mm SL); *Silurus asotus* BMNH Uncat. (cranium 65mm); 1983.7.6:13–19 Fukien (CS, 65mm SL); *S. glanis* BMNH Uncat. (S, crania, 105, 114mm), 148a (S, cranium 62mm); *S. triostegus* 1969.3.3:168–76 (Basrah (CS, 105mm SL; D, 215mm SL); *Wallago attu* BMNH Uncat. (S, cranium 98mm), 1891.11.30:156–161 Sittang R., (D, 350mm SL), Uncat. (S, cranium 84mm); LILI 89074 Weekend Market, Bangkok, Thailand (CS, 100mm SL); *W. leeri* BMNH 1880.4.21:203 No locality (D, 275mm SL, cranium extracted 57mm).

Other specimens examined: *Belodontichthys dinema* (syntype of *B. macrochir*) BMNH 1863.12.4:64 Borneo (266 mm SL);

ZMA 120.684 Sumatra (195, 210, 235, 245 mm SL); *Kryptopterus schilbeides* BMNH 1892.3.29:173 Kapuas (80 mm SL); *Ompok bimaculatus* ZMA 120.549 Orissa (145 mm SL), BMNH 1980.12.16:19 Vientiane (155 mm SL); *O. eugeneiatus* BMNH 1982.3.20:174 Kapuas (91 mm SL); *O. pabda* ZMA 15.541 Pakistan (91 mm SL).

Abbreviations used in figures

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A1, A2,	outer and inner divisions of *adductor mandibulae* muscle
aa	anguloarticular
AAP	*adductor arcus palatini* muscle
af	anterior fontanelle
afc	anterior branch of frontal canal
AH	*adductor hyomandibularis* muscle
afo	opening of anterior frontal canal
amf	adductor mandibulae fossa in pterotic
AO	*adductor operculi* muscle
apm	ascending process of premaxilla
apt	anterior pterygoid
AW	mandibular division of *adductor mandibulae* muscle
bo	basioccipital
bof	basioccipital facet
br	buccal ramus of trigeminal nerve
cco	cross-commissure opening
cl	cleithrum
cm	coronomeckelian bone
de	dentary
DO	*dilatator operculi* muscle
epo	epioccipital
EPX	epaxial muscle
ET	*extensor tentaculi* muscle
exo	exoccipital
fc	frontal crest
fco	opening of lateral branch of frontal canal
ff	facial nerve foramen
fg	glossopharyngeal foramen
fh	foramen for hyomandibular trunk of facial nerve
fhy	foramen for hyoid nerve
fim	foramen for internal branch of hyomandibular nerve
fm	foramen magnum
fo	foramen for optic nerve
fr	frontal
ft	foramen for trigeminal nerve
ftf	foramen for trigeminofacialis trunk
fv	foramen for vagus nerve
hy	hyomandibular
hyf	hyomandibular fossa
IM	*intermandibularis* muscle
io	infraorbital
lac	LAP crest on hyomandibular
LAP	*levator arcus palatini* muscle
le	lateral ethmoid
lea	lateral ethmoid articular facet
lfc	lateral branch of frontal canal
LO	*levator operculi* muscle
me	mesethmoid
mec	mesethmoid cornu
mo	mandibular canal opening
mx	maxilla
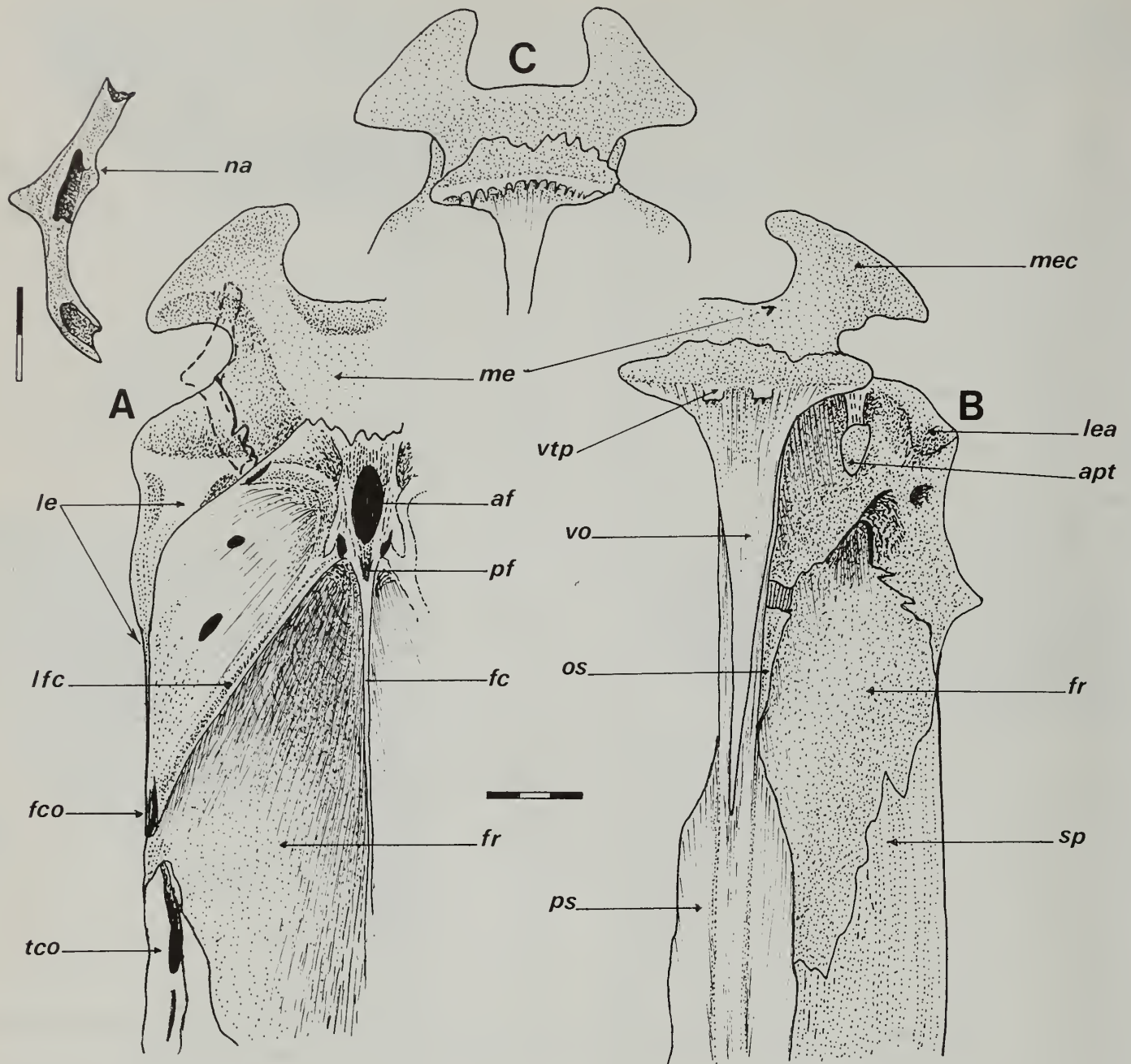
Fig. 2 *Belodontichthys dinema*: anterior part of neurocranium in A, dorsal and B, ventral views (51.5mm cranium, LILI 89008); C, ventral view of Indonesian specimen (34.5mm cranium IBRP 6625) showing difference in vomerine tooth pattern. In A, the nasal bone is shown shifted laterally and slightly enlarged; its position *in situ* is indicated by a dashed outline on the main figure. Scale bars on this and succeeding figures are in mm divisions.

na	nasal		pts	pterosphenoid
no	optic nerve		ptss	pterosphenoid shelf
os	orbitosphenoid		qf	quadrate foramen
pal	palatine		qu	quadrate
pf	posterior fontanelle		rme	external mandibular ramus of trigeminal nerve
pmx	premaxilla		rmi	internal mandibular ramus of trigeminal nerve
po	preoperculum		RT	*retractor tentaculi* muscle
ppt	posterior pterygoid		so	supraoccipital
pro	prootic		sp	sphenotic
prs	prootic spur		spo	supraoperculum
ps	parasphenoid		tcl	transcapular ligament
psc	posttemporosupracleithrum		tco	temporal canal opening in sphenotic
psk	parasphenoid keel		v1	1st vertebra
pss	parasphenoid shelf		vc	vertebral column
ptc	pterotic canal		vo	vomer
pte	pterotic		vtp	vomerine tooth patch pedestel

ANATOMICAL DESCRIPTIONS OF *BELODONTICHTHYS* AND COMPARISONS WITH OTHER MEMBERS OF THE SILURIDAE AND SILUROIDEI

Neurocranium (Figs 2–12)

In dorsal view the cranium is oblong, its lateral margins are straight without any noticeable protrusions (Figs 2, 3). The mesethmoid is wide with a deeply rounded indentation in the midline of its anterior border. The mesethmoid cornu is broad, and posteriorly is widely separated from the lateral ethmoid. The lateral ethmoid is deep medially with a round, ventrolaterally directed palatine articular surface. Posteromedially it meets the anterior border of the frontal and posterolaterally extends beneath the frontal to meet the anteriorly extended margin of the sphenotic.

The vomer has a laterally expanded head, the anterior part of which is angled upward against the axis of the parasphenoid; posteriorly, the vomer has a long shaft (v, Fig.

2B) which terminates beneath the anterior part of the pterosphenoid. The vomerine tooth patch pattern is variable. In our specimens of *B. dinema* from Thailand, the tooth patches are small, transversely aligned and, widely separated with two or three teeth borne on a long bony pedestal (vtp, Fig. 2B). In specimens from Indonesia, the tooth patch is continuous with ca 10 teeth, supported on a thin bony flange (Fig. 2C). Bornbusch (pers. comm.) has observed continuous tooth patches in specimens from Thailand.

The frontals are deeply concave in both transverse and longitudinal planes, their medial borders rise to join one another in the form of a deep crest (fc, Figs 2, 4). The anterior fontanelle is short and entirely enclosed by the frontals and elevated between the paired frontal crests. The posterior fontanelle (pf) is narrowly separated from the anterior one (af) and has the appearance of a small foramen; it too is enclosed by the frontal crests (Figs 2, 4). Ventromedially, the frontals slope toward the midline where they meet the orbito- and pterosphenoids. Laterally each frontal is bordered partially by the sphenotic, posteriorly by the pterotic and medially by the supraoccipital (so, Figs 2, 3).
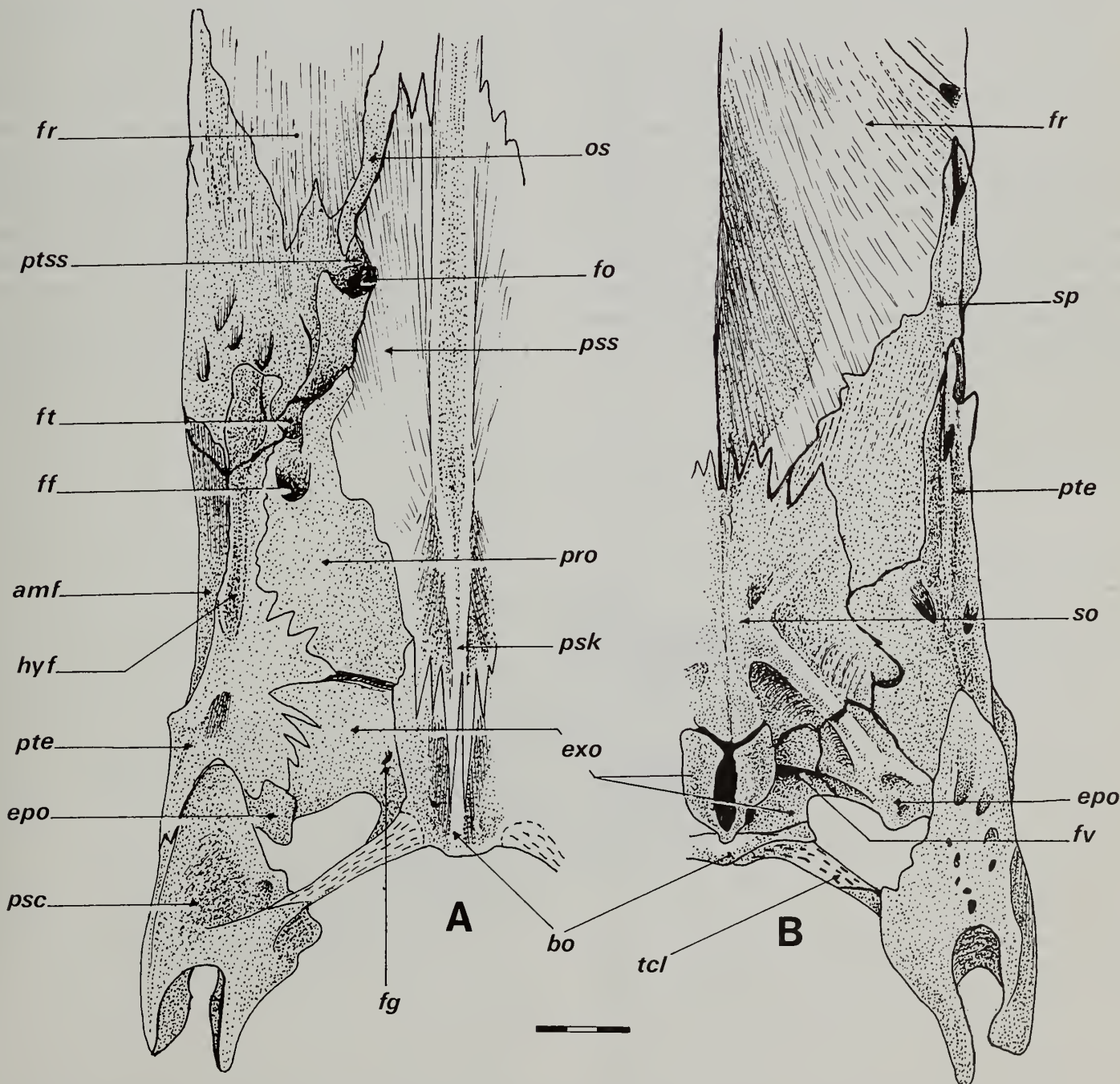

Fig. 3 *Belodontichthys dinema*: posterior part of neurocranium in A, ventral and B, dorsal views (LILI 89008).

The frontal sensory canal is short and runs diagonally from the anterior fontanelle to the anterior border of the bone where it meets the nasal canal. Owing to the trough-like contour of the anterior part of the frontal the course of the canal is strongly curved. A posterior branch of the canal extends from the posterior fontanelle and follows a diagonal course to the posterolateral border of the bone where it forms a tripartite connection with the infraorbital and temporal canals (lfc, Fig. 2A).

The sphenotic (sp., Fig. 3B) borders the posterolateral margin of the frontal but anteriorly is separated by that bone from the lateral ethmoid. Ventrally, the sphenotic contains the anterior part of the hyomandibular fossa. The cranial surface of the pterotic is concave, its raised lateral margin bearing the sensory canal. Posteriorly the border of the pterotic is indented where it meets the posttemporosupracleithrum; medially it contacts the supra- and epioccipitals; its ventral surface contains two long fossae, the upper for the origin of the *adductor mandibulae* muscle, the lower for the articulation of the hyomandibular (dmf hyf, Figs 3, 5).

The supraoccipital is a large anteriorly sloping bone that bears a shallow medial crest is continuous with that of the frontal; the semicircular canal tube is raised well above the bone's surface and runs posterolaterally to join the similarly elevated canal tube of the square-shaped epioccipital (epo, Figs 3B, 5). The exoccipital contributes to the dorsal surface of the cranium between the supra- and epioccipitals; posteriorly it is perforated by an extensive vagus foramen and posteromedially rises to border the supraoccipital (Fig. 6A). Its ventrolateral face is perforated by the glossopharyngeal foramen (fg, Fig. 3B). The basioccipital is short with a slight median keel (bo. Figs 3, 5); its exposed lateral surface is joined to the ventral (ligamentous) limb of the posttemporosupracleithrum. The only part of the basioccipital exposed dorsally is that forming the rim of the vertebral articular condyle which has an oblate outline (Fig. 6A).

Both the orbito- and pterosphenoids are shallow plate-like bones, the former contacting the frontal dorsally, the latter, both the frontal and sphenotic; ventrally the bones are sutured with the parasphenoid. The pterosphenoid is perforated centrally by the optic foramen which has a cowl-like dorsal shelf, and posteriorly its border forms part of the trigeminal foramen (ptss, Figs 3A, 5).

The prootic is a somewhat bullate bone, its anterior border forming the lateral part of the trigeminal foramen (ft). Lying close to the margin of that opening is a separate foramen for the hyomandibular branch of the trigeminal nerve trunk (Figs 3A, 5).

The parasphenoid has a marked ventral keel and its orbital part is angled upward relative to the vertebral axis. Ventral to the pterosphenoid the parasphenoid has a lateral, shelf-like expansion (pss, Fig. 3A). The otic part of the bone is broadly expanded to contact the prootics and the keel is continued posteriorly to the basioccipital (psk, Figs 3A, 5).

Comparisons

The neurocranium of *Belodontichthys* differs in several respects from that of other members of the Siluridae. The most marked of the differences are the sharply angled ventral surface of the vomer-mesethmoid, the keel-like and upwardly angled parasphenoid, the cavernous nature of the frontals and the modification of the sensory canals in the frontals.

The upward slope of the mesethmoid and thick cornua are otherwise only found in *Ompok* and *Wallago* (Fig. 7); in other silurid taxa the ethmoid has a horizontal ventral surface and narrow, pointed cornua with, in most *Kryptopterus* and all *Silurus* species examined, a slight posterior curvature (Fig. 8B). In *Hemisilurus* and *Kryptopterus moorei* the cornua are straight. The large, ventrally directed palatine articular surface of the lateral ethmoid of *Belodontichthys* is a feature also shared with *Ompok* (Fig. 8A). In *Wallago* and *Silurus*,
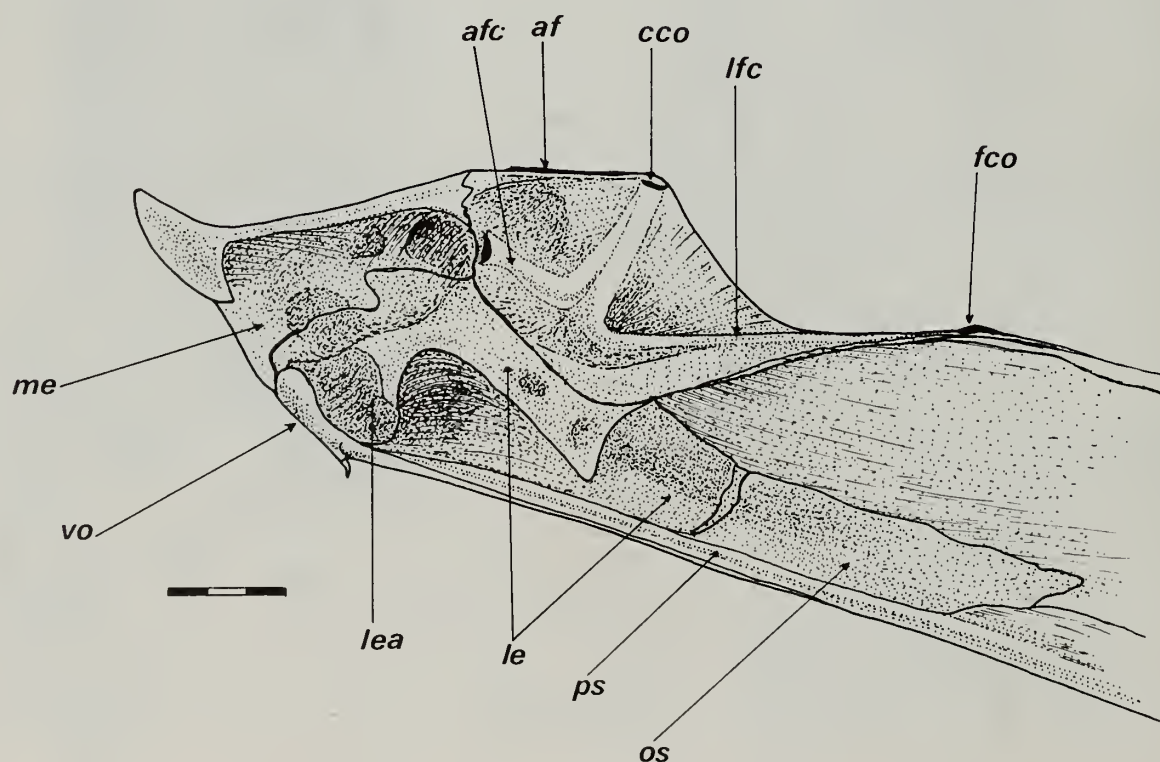

Fig. 4   *Belodontichthys dinema*: ethmoid region in left lateral view; shown in correct orientation relative to vertebral axis (LILI 89008).
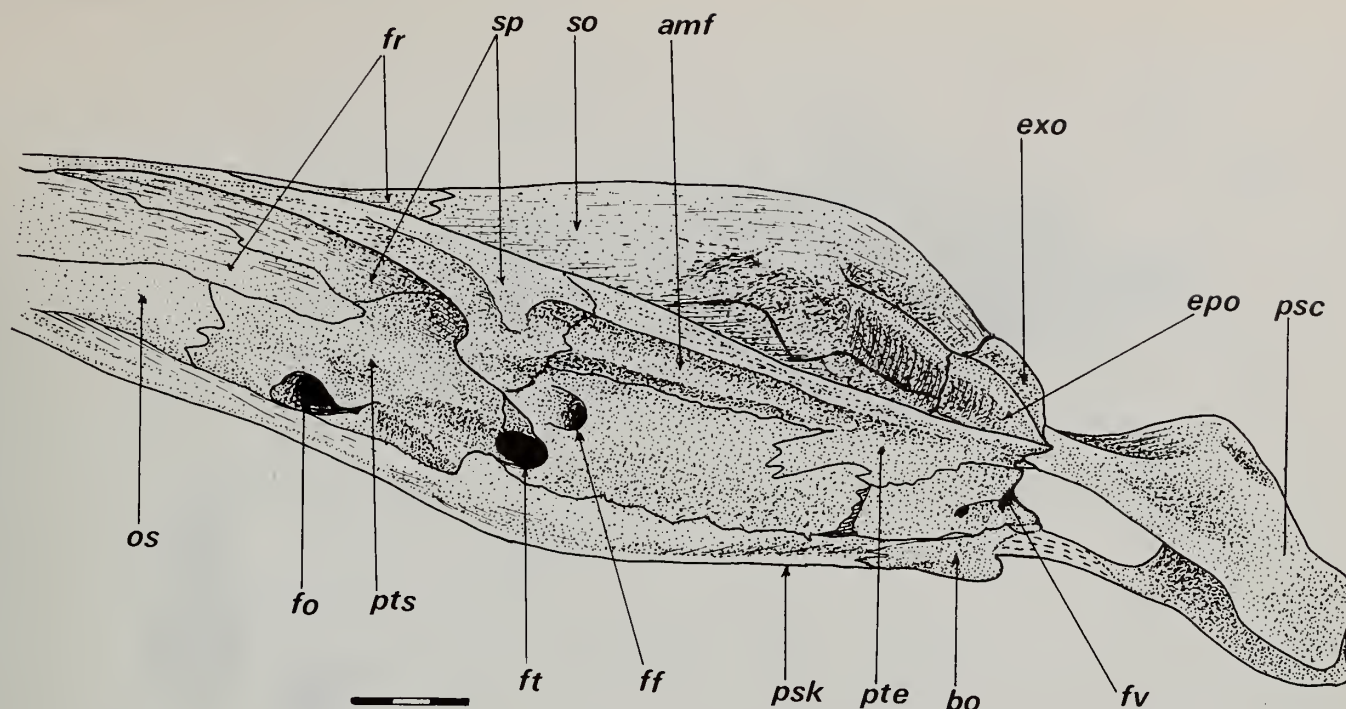
Fig. 5 *Belodontichthys dinema*: posterior part of neurocranium in left lateral view with posttemporosupracleithrum attached; shown in correct orientation relative to vertebral axis (LILI 89008).

although this articular surface is large, it is directed antero-laterally while in other silurid taxa it is small and situated laterally (Fig. 8B), i.e., the widespread and assumed plesio-morphic siluroid condition (Arratia, 1987; Bornbusch pers. comm.). The ventrally directed articulatory facet of the lateral ethmoid in *Belodontichthys* and *Ompok* is thus taken to be synapomorphic for these two taxa.

In its narrow head and upwardly sloping anterior surface, the vomer is also like that of *Ompok* and *Wallago*, however, in the latter genus the anterior border of the vomer is triangular rather than straight. A straight anterior border to the vomer is present in *Hemisilurus* and *Kryptopterus moorei*. *Ompok bimaculatus* resembles *Belodontichthys* in having narrow, transverse tooth patches bearing teeth carried on a bony flange (Fig. 8A). In some species of *Silurus* and *Kryptoperus* the vomerine tooth patch forms a continuous curved band but in *Wallago* and other *Silurus* species the band is V-shaped and interrupted in the midline to form two separate patches (Joseph, 1958; Kobayakawa, 1989).

Among siluroids vomerine tooth patches occur either paired or as a single, usually crescentic, band on either side of the vomerine head. Which of these conditions is the more derived is difficult to determine since both have equal distri-bution in the (admittedly restricted) number of taxa we have examined. Large, paired tooth patches occur in assumed plesiomorphic siluroids (Diplomystidae, Arratia, 1987; Hypsidoridae, Grande, 1987). Since vomerine teeth do not occur in other otophysans, out-group comparison does not aid in polarity assignment. Ontogenetic evidence suggests that the paired condition might be the more plesiomorphic since in post-larval *Clarias gariepinus* (which have a con-tinuous band of teeth in adults) we have examined paired ossification centres precede the development of the teeth. In the largest specimen of the ontogenetic series examined (28mm SL) the tooth-bearing patches are still separated medially. We therefore suspect that the separated tooth patches represent the plesiomorphic siluroid condition (see also Bornbusch & Lundberg, 1989, fig. 6). Nonetheless, we also consider the reduced, transverse and pedestal-like

process to be derived states of the vomerine tooth-patch type shared by *Belodontichthys* and *Ompok*.

No other silurid (or even siluroid) possesses the deeply concave frontal morphology of *Belodontichthys* but a partial excavation (concavity) of the posterior part of the frontal occurs in *Ompok* and *Wallago*. These latter genera also resemble *Belodontichthys* in having a short and narrow anterior fontanelle and high frontal crests. *Belodontichthys* is, however, unique in having the fontanelle entirely enclosed by the frontals and not extending anteriorly into the ethmoid. In *Belodontichthys* and *Ompok* the crest declines posterior to the fontanelle and becomes continuous with the supraoccipital crest (Figs 4, 7). In *Wallago* the crest remains elevated and in other members of the Siluridae takes the form of paired ridges which gradually rise from their origin to border the posterior fontanelle before meeting the supraoccipital crest.

Normally in siluroids the frontal sensory canal (supra-orbital canal) runs along the medial part of the bone, diverg-ing anteriorly to terminate where the nasal contacts the anterior border of the frontal. Posteriorly, the canal bifurcates, its medial branch (termed cross-commissure or parietal branch) enters the depression that lies between the anterior and posterior fontanelles and either opens in a pore or remains enclosed in the bony epiphysial bar which com-municates with its contralateral partner. The lateroposterior branch joins the temporal canal of the sphenotic, *viz*. the plesiomorphic condition as exemplified in Diplomystidae (Arratia, 1987). In the Siluridae, the cross-commissure enters a channel formed between the raised frontal crests and there is no lateroposterior branch. Instead, an anterolateral branch extends forward to open on the frontal border above the centre of the orbit. The upper infraorbital bone appears to have a subcutaneous connection with this anterolateral branch as well as the temporal canal (Figs 9, 10). In *Silurus, Silurichthys* and *Kryptopterus* this branch of the canal is moderately divergent from the medial frontal canal but in *Wallago* the canal extends transversely from the midline (Fig. 9A) and in *Ompok* is curved posteriorly to form a crescentic ridge across the frontal (Fig. 10A).
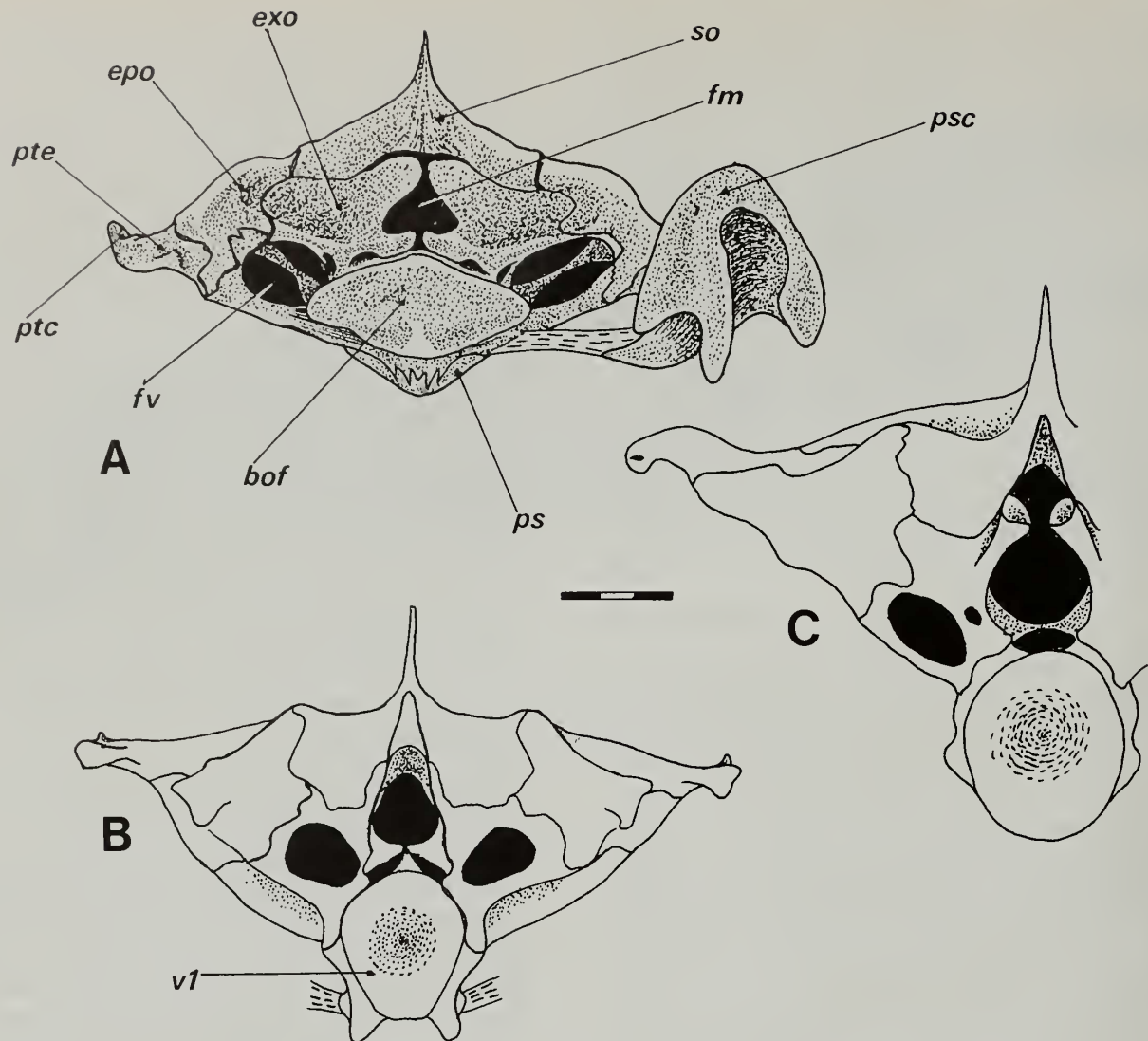
Fig. 6 Neurocrania in posterior view of A, *Belodontichthys dinema* (LILI 89008); B, *Ompok bimaculatus* (1891.11.20:171–8); C, *Wallago leeri* (1880.4.21:203).

In *Belodontichthys*, the canal branch extends postero-laterally, having a reversed orientation relative to that of other silurids but nonetheless still retains the lateral pore opening in the same position, *viz* midway along the edge of the frontal and above the orbit, the opening interconnecting with those of the sphenotic and infraorbital canals (see above and Fig. 2A). The lateroposterior orientation of the canal branch in *Belodontichthys*, *Ompok* and *Wallago* we consider as a shared derived state (see further discussion on p. 155).

In *Belodontichthys* the sphenotic is separated dorsally from the frontal by the lateral ethmoid, but the bones are in contact ventrally (Figs 2A, B). In other silurids examined the entire anterior margin of the frontal contacts the lateral ethmoid, a condition (first noted by Regan, 1911) not encountered elsewhere in siluroids and one considered synapomorphic for the Siluridae (Bornbusch, 1988; 1990). Kobayakawa (1989) figures the frontal in *Silurus mento*. *S. cochinchinensis*. *S. grahami and S. microdorsalis* as forming the lateral orbital border of the cranium, at least dorsally; if this is so, then the distribution of this character is incongruent with others shown in her cladogram of relationships. Bornbusch (pers. comm.) notes that there is variability within silurid taxa with respect to the degree of dorsal exposure of the frontal along the orbital margin.

The raised lateral border of the pterotic in *Belodontichthys* is a feature shared with *Ompok*. In both those taxa the sensory canal comes to lie along the 'medial' surface of the elevated border (Fig. 6A, B). In *Silurus* and *Wallago* (Fig. 6C) the pterotic border is also slightly raised but in other genera the border and its associated sensory canal remains flat. *Hemisilurus* is exceptional in that it too has an elevation of the pterotic, but here the canal runs lateral to the elevation which can thus be considered as a ridge rather than the pterotic margin.

The narrow orbital keel of the parasphenoid with its sharp midline ridge meeting the basioccipital (Figs 5, 7) are derived features (*Belodontichthys* shares only with *Ompok* among other examined silurids. In other Siluridae, the parasphenoid keel is broad and flat but both *Silurus* and *Wallago* share with *Belodontichthys* and *Ompok* a lateral expansion of the parasphenoid keel which meets posteriorly a similar shelf of the pterosphenoid (pss, pts, Fig. 11B). In no other taxon is the parasphenoid as sharply angled with respect to the vertebral axis as in *Belodontichthys*, although a pronounced but lesser angle occurs in *Ompok* (Fig. 7).

In *Belodontichthys* and *Ompok* the pterosphenoid is deeply indented where it meets the prootic, and its anteroventral border is extended anteriorly to form a somewhat tube-like opening for the optic nerve (Figs 5, 7).

In siluroids there is usually only a single opening for the trigeminal nerve trunk (a siluroid synapomorphy). *Belodontichthys* shares with *Kryptopterus* and *Hemisilurus* the presence of a secondary foramen in the prootic, through which passes the hyomandibular branch of the VII cranial
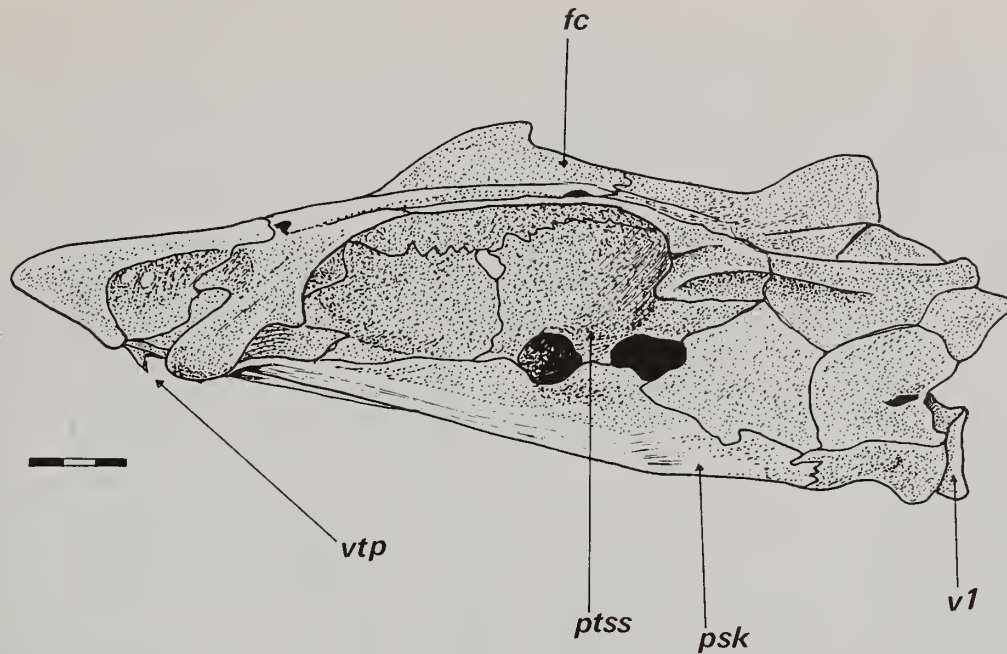
Fig. 7 *Ompok bimaculatus*: neurocranium in left lateral view (shown in correct orientation relative to vertebral axis); only those features of particular significance and discussed in the text are indicated (BMNH 1891.11.20:171–8).
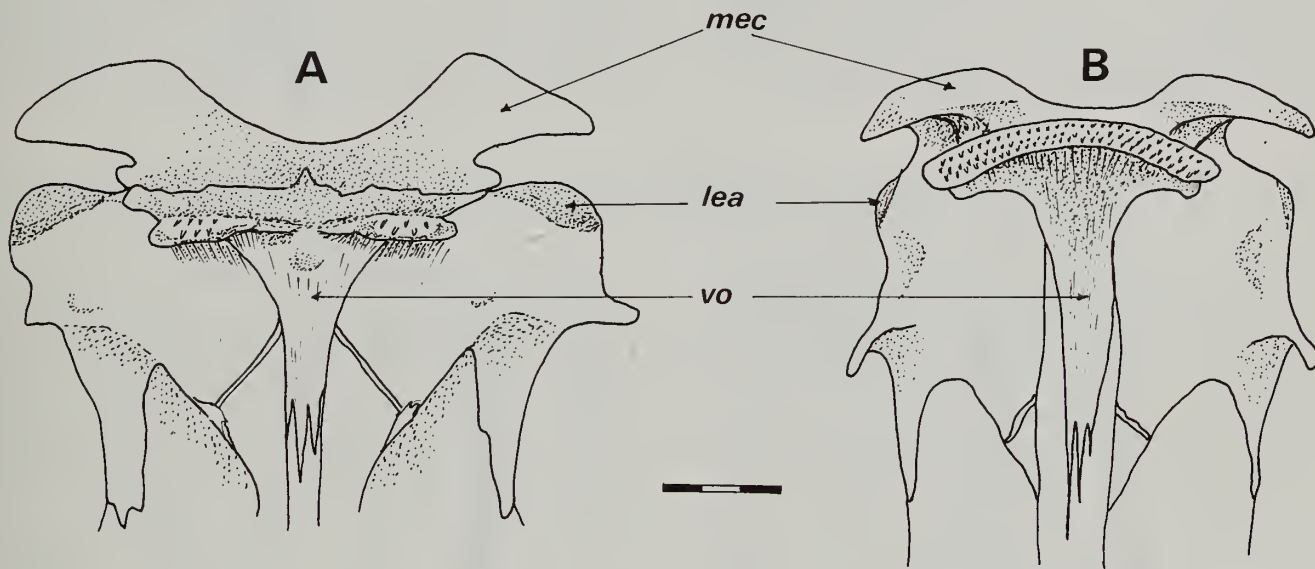

Fig. 8 Ethmoverine region in ventral view of, A, *Ompok bimaculatus* (BMNH 1891.11.20:171–8); B, *Kryptopterus bleekeri* (LILI 89030).

nerve (Figs 5, 12A). *Ompok* lacks this condition, as do other silurids investigated. *Silurus*, however, displays both conditions. In three specimens of *S. glanis*, one has a single trigeminal opening, although it is partially divided by a bony spur extending anterodorsally from the prootic (Fig. 12B), and two have a secondary foramen for the hyomandibularis nerve formed by a complete suture between a prootic process and the pterosphenoid (Fig. 12C). In *S. asotus* a prootic spur extends ventrally from the dorsal rim of the trigeminal opening (Fig. 12D). An accessory foramen for the hyo-mandibular branch of the trigeminal trunk also occurs in *Hypophthalmus* (Hypophthalmidae) (Howes, 1983:22) and has been reported in Pimelodidae by Lundberg *et al.* (1990). We have also found this condition in a specimen of *Chrysichthys cranchii* (Bagridae). The presence of an additional foramen in the prootic is considered to be a derived feature. In *Belodontichthys* as in other Siluridae the optic and trigeminal foramina are widely separated by a bony wall, but in *Hemisilurus* the separation is membraneous.

The occipital roof is somewhat flattened in *Belodontichthys*,

Ompok, Wallago and *Silurus* but in *Hemisilurus* and *Kryptopterus* it is pinnacle-shaped. In all these taxa apart from *Silurus*, the epi- and supraoccipital semicircular canal tubes are elevated to form a high, posterior ridge to the cranial roof whereas in *Silurus* the canals are indicated only as slight ridges along the posterolateral margins of those bones. In all siluroids the exoccipital forms the lower posterior wall of the cranium; the lateral part of the bone lies in the transverse plane while the medial part turns at right angles to extend posteriorly beneath the supraoccipital. In the Siluridae the exoccipital, rather than being vertical as in the majority of siluroids, slopes backward so that it is visible from above. In all silurids other than *Silurus*, the dorsal part of the exoccipital is flat and contributes to the cranial roof. An apparent correlate of this arrangement is the reorientation of the vagus nerve foramen. Typically in siluroids the foramen perforates the posterior part of the lateral face of the bone. In *Silurus*, the foramen lies at the posterior margin of the bone (Fig. 11A); in other silurids it is located on the bone's posterior face and has the appearance of a posttemporal

fossa. In *Silurichthys* and *Belodontichthys* the depression is extensive (Fig. 6A). The true posttemporal fossa in siluroids is a small cavity floored by the pterotic and roofed by the epioccipital, its opening usually occluded by the extrascapular and/or posttemporosupracleithrum. In Siluridae and Schilbeidae, however, a posttemporal fossa is absent (T.P. Mo pers. comm.).

The basioccipital is short in all Siluridae, its anterior ventral margin which contacts the parasphenoid, lying in line with the exoccipital-prootic suture and not as in many other siluroids lying beneath the centre of the prootic. The silurid condition may, however, be plesiomorphic since a short basioccipital occurs in Diplomystidae (Arratia, 1987). *Belodontichthys* appears unique amongst the members of the Siluridae in the oblateness of its basioccipital condyle (Fig. 6A).

In most silurids the medial arm of the posttemporosupra-cleithrum (transcapular) is compressed and well-ossified, but in *Kryptopterus, Wallago* and *Silurus* it has a long ligamentous connection to the basioccipital proximally *Belodontichthys* has an almost entirely ligamentous transcapular (Figs 3, 6). The posteroventral bifurcated portion of the posttemporo-supracleithrum, into which the cleithrum fits is vertical in *Belodontichthys*, whereas in other Siluridae and the majority of siluroids it is directed somewhat laterally, as is the upright limb of the cleithrum; the *Belodontichthys* condition is reckoned to be the more derived. In common with other silurids, *Belodontichthys* lacks separate extrascapulars.

The jaws (Figs 13–16)

The maxilla is a long tapering bone with a transversely convex dorsal surface; its underside bears a longitudinal ridge (Fig. 13B, C). The head of the maxilla is flat, with double articulatory facets which contact the lateral border of the palatine. The premaxilla is angled at 45° to the midline; it is rather short and has a narrow dentigerous surface (Fig. 14A). The teeth are arranged in three irregular rows, the outer row teeth are the shortest and number 15–18, the inner and middle rows both number 9–10 and the teeth are nearly twice the length of those in the outer row, those of the innermost row being directed posteriorly. All the teeth have flattened, arrow-shaped tips (Figs. 14A).

The lower jaw is long, the length of the anguloarticular being 50% that of the entire jaw (Fig. 15). The dentary is shallow and rises posteriorly to form with the anguloarticular, a slight coronoid process. The dentigerous surface is narrow and bears three rows of teeth anteriorly and two rows posteriorly, the middle row extends only a short way along the surface. The outer row teeth number 16–18 which are short anteriorly but long posteriorly. The inner row teeth number 14–20, are markedly elongate and inwardly curved and long anteriorly and short posteriorly. The middle row teeth number 9–18 and are the same size as the anterior inner row teeth and, like them are recurved. All the dentary teeth have arrow-shaped tips. The dentary has a deep, anteriorly
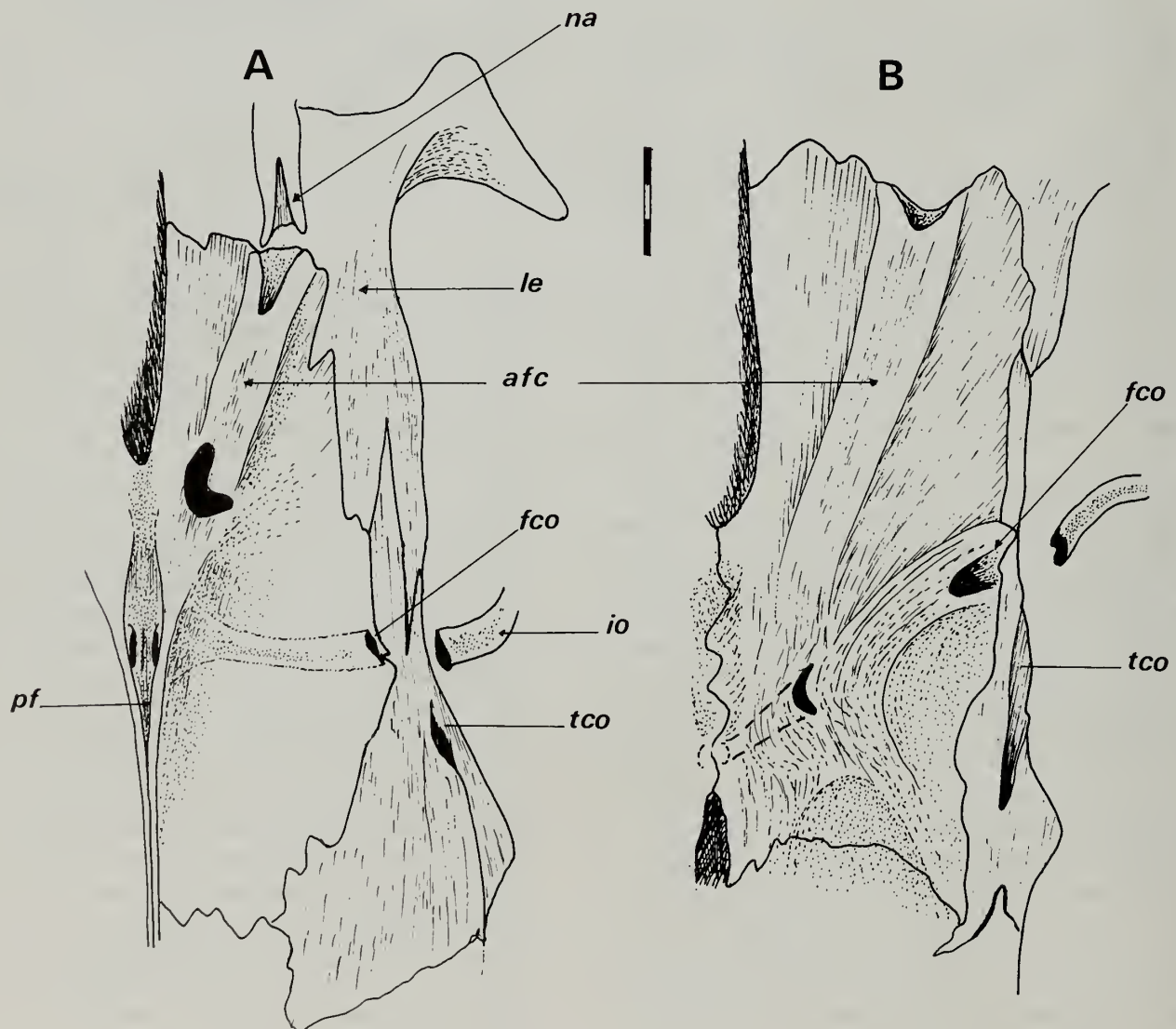

Fig. 9 Frontal and temporal sensory canals in A, *Wallago attu* (BMNH Uncat.); B, *Silurus glanis* (BMNH Uncat.).
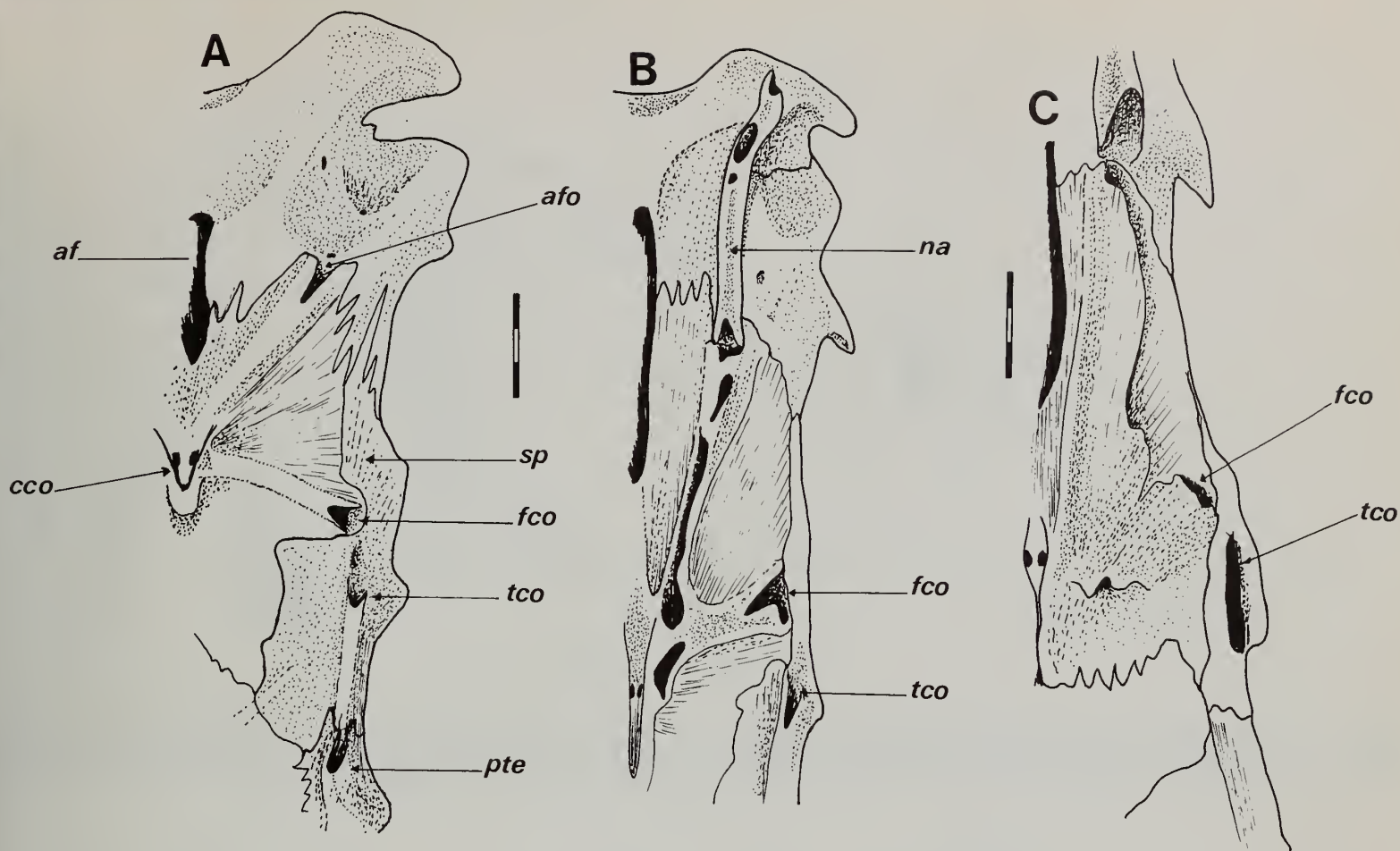
Fig. 10 Frontal and temporal sensory canals in A, *Ompok bimaculatus* (BMNH 1891.11.20:171–8); B, *Kryptopterus bleekeri* (LILI 89030); C, *Hemisilurus heterorhynchus* BMNH 1982.3.29:161.

extended mentomeckelian cavity; a small coronomeckelian bone lies in the posterior cavity of the anguloarticular from which the Meckelian cartilage extends forward. The anguloarticular is deep, its dorsal border lying at the same level as that of the dentary, forming a smoothly rounded coronoid process. The anterior border of the anguloarticular extends well forward into the mentomeckelian cavity of the dentary. The articulatory surface is complex, with a large, inwardly angled facet (Fig. 15C).

In keeping with the condition in other members of the Siluridae and the majority of siluroids examined, the premaxilla of *Belodontichthys* is approximately half the length of the lower jaw. The laterally exposed surface, i.e. the part not covered by the ethmoid cornua, is 45% of its total length. In comparison, the exposed surface in other silurid taxa ranges from 25% (*Kryptopterus apogon*) to 40% (*Ompok bimaculatus*). The premaxillary ascending process, which contacts the lateral margin of the ethmoid cornua, is a rather prominent, obliquely transverse process in *Belodontichthys* and *Ompok*, whereas in other Siluridae it rises gently to a promontory situated in the centre of the bone (Figs 14A–D).

The lower jaw of *Belodontichthys* differs markedly from that in other genera of Siluridae and the majority of siluroids in having only a slight inward curvature at the symphysis (Fig. 15D); in other taxa the united rami form a broad crescent or a U-shape. The dentary differs little in its length and depth from that in other Siluridae and, like most, has 5 openings in the sensory canal. *Silurus* and *Wallago* have between 6 and 10. The dentary canal openings in *Hemisilurus* and *Ceratoglanis* (Bornbusch & Lundberg, 1989) are extensive and separated from one another by narrow bony struts (Fig. 16C). The moderate development of the coronoid process of

Belodontichthys agrees with that in most siluroids. According to Lundberg (1970) and Grande (1987) an elevated coronoid process is the more derived siluroid condition. However, a high process is also present in Diplomystidae (Arratia, 1987), and among the Siluridae a reduced coronoid process appears to be a derived condition associated with increased jaw length (i.e. *Silurus* and *Wallago*). The articular surface of the anguloarticular in all genera of the Siluridae apart from *Wallago* and *Belodontichthys* bears a transverse facet which in these two genera is obliquely angled. No other silurid taxon has such a complex articular surface as *Belodontichthys* (Fig. 15C).

In all members of the Siluridae, apart from *Belodontichthys*, *Ompok* and *Kryptopterus moorei*, the dentigerous areas of the jaws are broad, the teeth ranging from short, stout and conical (*Hemisilurus*, *Silurichthys*) to long and caniniform, the most derived state being exemplified by *Belodontichthys* (see above). A series of elongate inner row teeth is a feature shared not only with *Ompok*, *Silurus* and *Wallago* but also with two *Kryptopterus* species, *K. micronema* and *K. kryptopterus*. In these latter taxa, however, the elongate teeth are widely separated from each other by three or four uniformly sized smaller teeth whereas in the other three genera all the teeth are elongate and regularly spaced. Of the other *Ompok* species we have examined, *O. pabda* is the only one, apart from *O. bimaculatus* which has equally sized elongate inner-row teeth. We assume this condition to be synapomorphic for *Belodontichthys*, *Ompok* (in part), *Silurus* and *Wallago*. On the basis of the different condition of the irregularly spaced teeth in *Kryptopterus* and the incongruence of other synapomorphies (p. 153) we hypothesise that the *Kryptopterus* condition is independently derived.
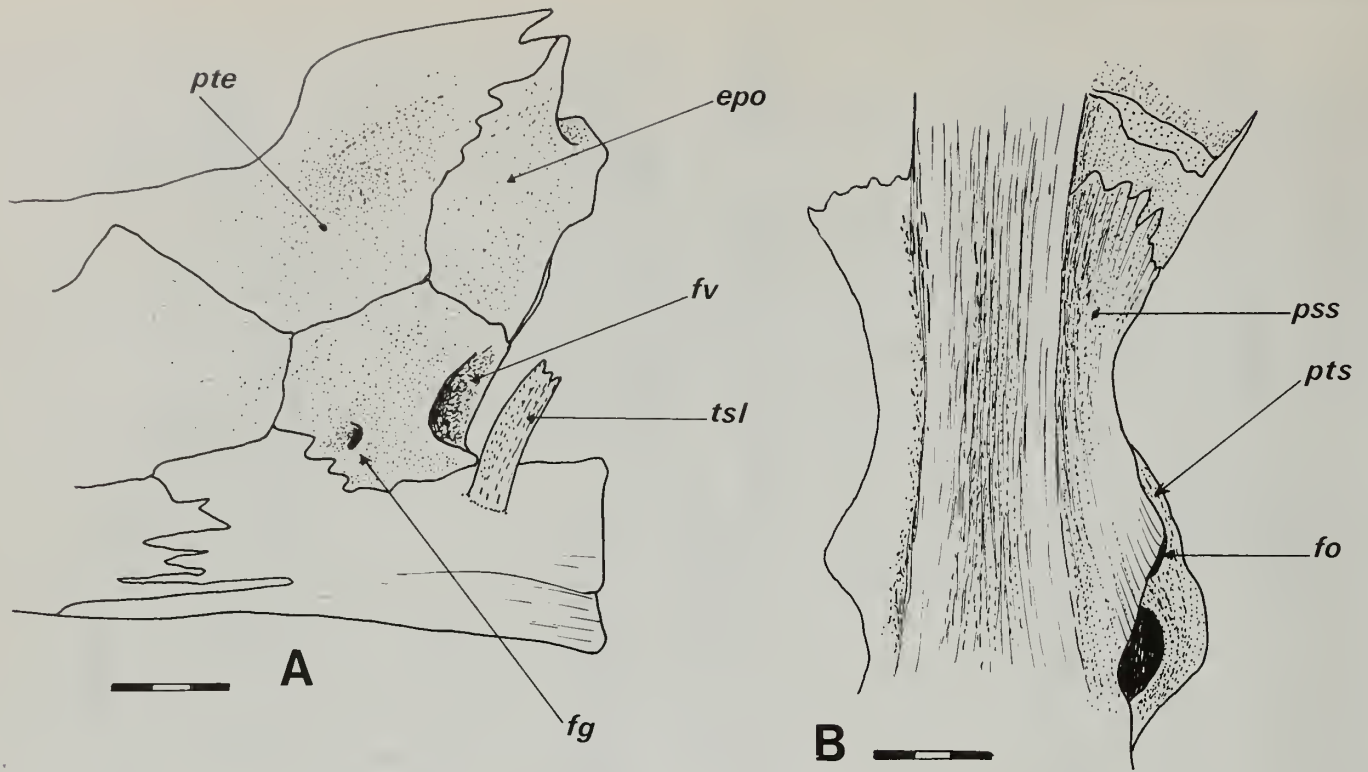
Fig. 11 A. *Silurus asotus*: posterior part of neurocranium in lateral view showing position of vagus foramen (transcapular ligament cut); B, *Silurus glanis*: orbital region of parasphenoid in ventral view to show shelf (BMNH uncat. specimens).
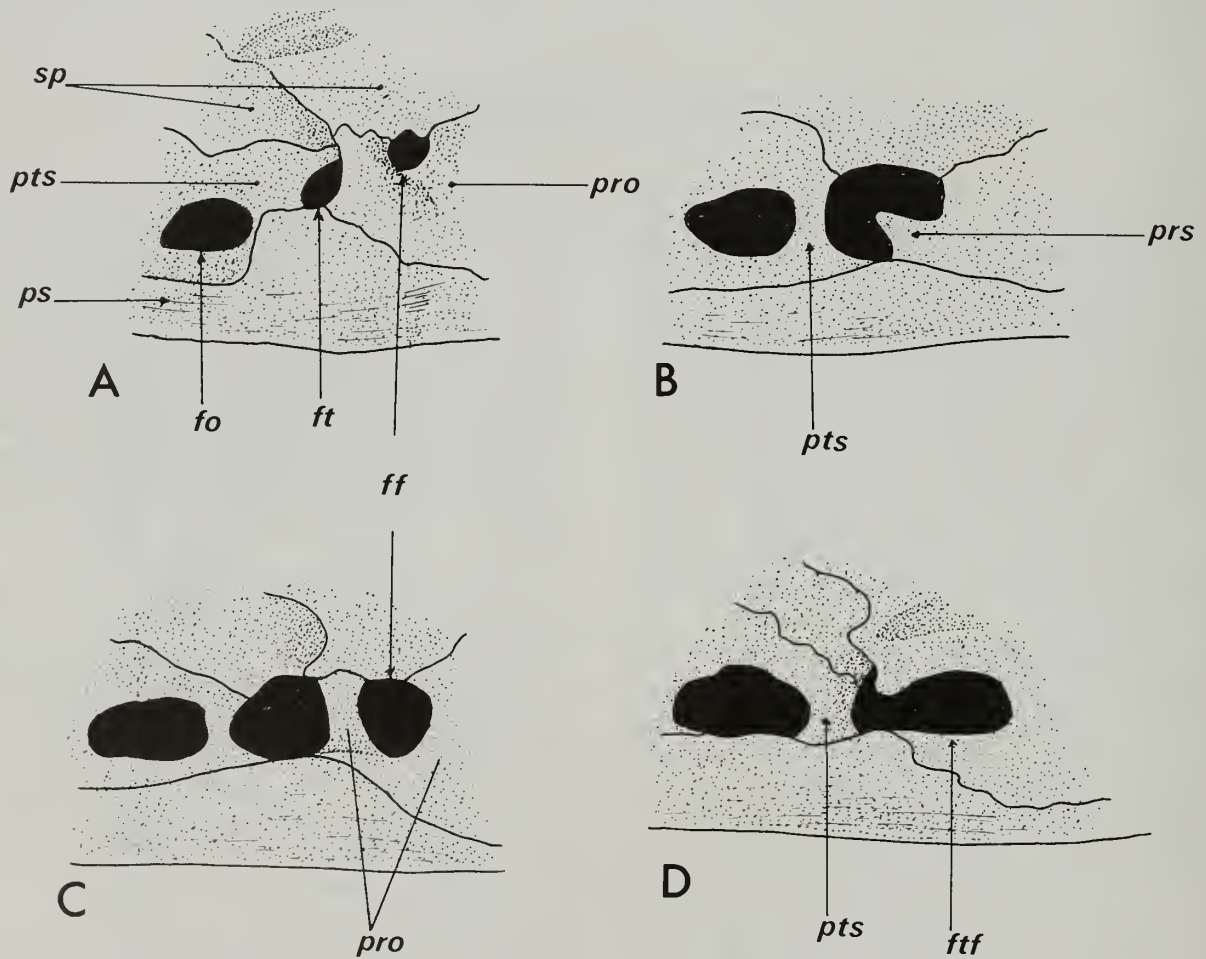

Fig. 12 Trigeminal and facial nerve foramina in A, *Kryptopterus bleekeri* (LILI 89016); B, *Silurus glanis* (114mm cranial length); C, *S. glanis* (105mm CL); D, *S. asotus* (65mm CL; all BMNH Uncat.).

Hyomandibular and palatoquadrate (Fig. 17)

Relative to the condition in other genera, the hyomandibular is somewhat higher than broad, has a horizontal dorsal articulatory surface, and an irregularly concave anterior border. A strong vertical crest with a concave anterior border extends down the anterolateral face in front of the hyomandibularis nerve foramen (Fig. 17A). Posteriorly, there is
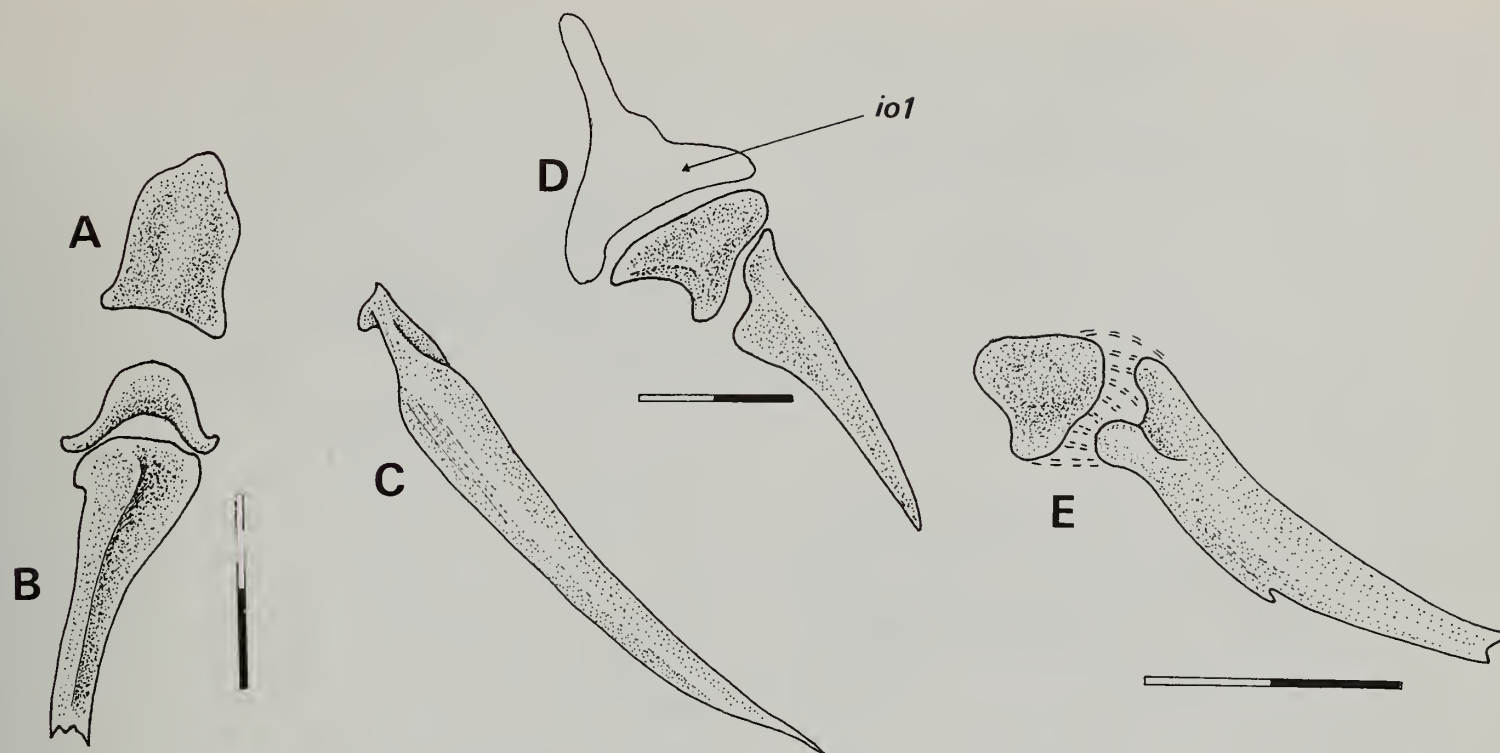
Fig. 13 *Belodontichthys dinema*: A, palatine (right) in dorsal view; B, palatine and maxillary head (anterior view of articulation); C, maxilla (right) in lateral view (LILI 89002); D, *Ompok bimaculatus,* palatine with maxilla (right), shown *in situ* with respect to 1st infraorbital (BMNH 1891.11.20: 171–8); E, *Wallago attu,* palatine and maxilla (right) in articulation and bound by connective tissue (double-dashed lines) LILI 89074.

a well-developed opercular condyle; ventrally, the bone is indented by the foramen for the mandibularis branch of the hyomandibular nerve and is covered by the properculum. The quadrate is large with (in cross-section) a triangular articular condyle whose articulatory surface is deeply divided (Fig. 17A). The posteroventral surface of the quadrate is covered by the lower part of the preoperculum. There are two pterygoid bones, an extensive posterior element which contacts, respectively, the anterior and dorsoanterior margins of the hyomandibular and quadrate, and a small, oblong element ligamentously suspended between the large pterygoid and the lateral ethmoid (ppt and apt, Fig. 17A).

Comparisons

Compared with other members of the Siluridae, *Belodontichthys* has a narrower hyomandibular with a more pronouncedly concave anterior border. The longitudinal lateral crest also has a marked concave anterior margin and its ventral surface serves as the site of insertion for the *levator arcus palatini* muscle and origin of the inner section of the *adductor mandibulae* muscle. A prominent longitudinal LAP crest also occurs in *Ompok* (Fig. 17E) but in other Siluridae apart from *Wallago* it is reduced to a narrow bar. In *Wallago attu* the width of the crest is such that it extends forward as a long pointed lamina of bone to overlap the posterolateral face of the large pterygoid (Fig. 17E), whereas in *W. leeri* the crest is much narrower and more closely resembles the condition in *Silurus* (Fig. 17C, D). Generally, in siluroids, if a lateral crest or ridge for the insertion of the LAP occurs at all, it is horizontal or subhorizontal (Lundberg, 1970; Grande, 1987) and we have found a similar vertical ridge to be present only in the schilbeids, *Proeutropiichthys* and *Eutropiichthys*. According to Bornbusch (1990) the vertical crest in Siluridae is not homologous with the horizontal (LAP) crest in other siluroids since it serves principally as the site of adductor

muscle origin. As noted above, however, the LAP crest is sometimes subhorizontal and also acts as an area of attachment for the adductor musculature. Thus it seems to us that the vertical ridge or flange in Siluridae is a reorientated LAP crest. As such this feature is considered synapomorphic for the Siluridae and the enhanced development of the crest in *Belodontichthys, Ompok* and *Wallago* is taken to represent a further derived condition for these taxa (see also under quadrate).

The dorsal articular surface of the hyomandibular in siluroids almost always bears an anterior process which articulates with the sphenotic; the size and degree of medial tilt of the process are variable (Lundberg, 1970). In the Siluridae, however, the anterior dorsal process is, apart from *Silurus*, reduced (Bornbusch, 1988). *Silurus* retains the plesiomorphic condition in which the process is large and almost vertical (Fig. 17D). The specimens of *Belodontichthys* and *Ompok bimaculatus* that we have examined lack a dorsoanterior process, although a small cartilaginous process is present in a cleared and stained preparation of the former and a minute, medially directed process is present in other *Ompok* species examined.

The large, posterior pterygoid bone in siluroids is generally referred to as the metapterygoid. Since the homologies of this and the other pterygoid elements in siluroids have not been firmly established (Arratia, 1987; Howes & Teugels, 1989) we refer simply to posterior and anterior pterygoids. Only two pterygoids occur in Siluridae, the anterior of which is always reduced and is either situated distant from the anterior border of the posterior pterygoid (*Belodontichthys, Ompok*) or closely associated with it (other Siluridae; cf. Figs 17A, F and B, E); in either case it is ligamentously attached to both the posterior pterygoid and the lateral ethmoid. The shape and size of the anterior pterygoid is also variable and may be large and plate-like (*Wallago*), rod-shaped (*Silurus*) or a short, oblong lamina (other taxa); Figs 17B–E.
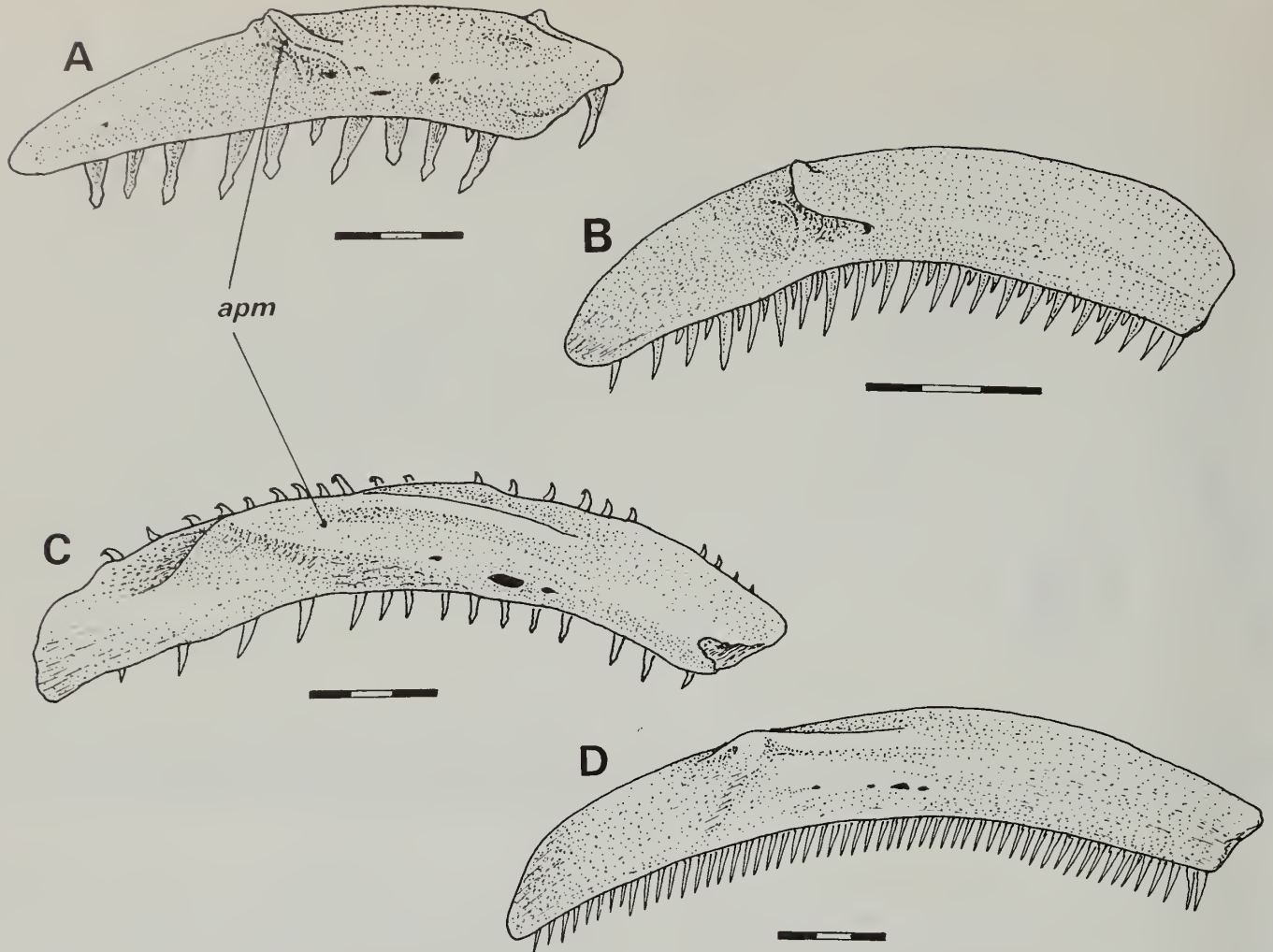
Fig. 14 Premaxillae (left): posterodorsal views of A, *Belodontichthys dinema* (LILI 89008); B, *Ompok bimaculatus* (BMNH 1891.11.20:171–8); C, *Kryptopterus apogon* (LILI 89016); D, *Wallago leeri* (BMNH 1880.4.21:203).
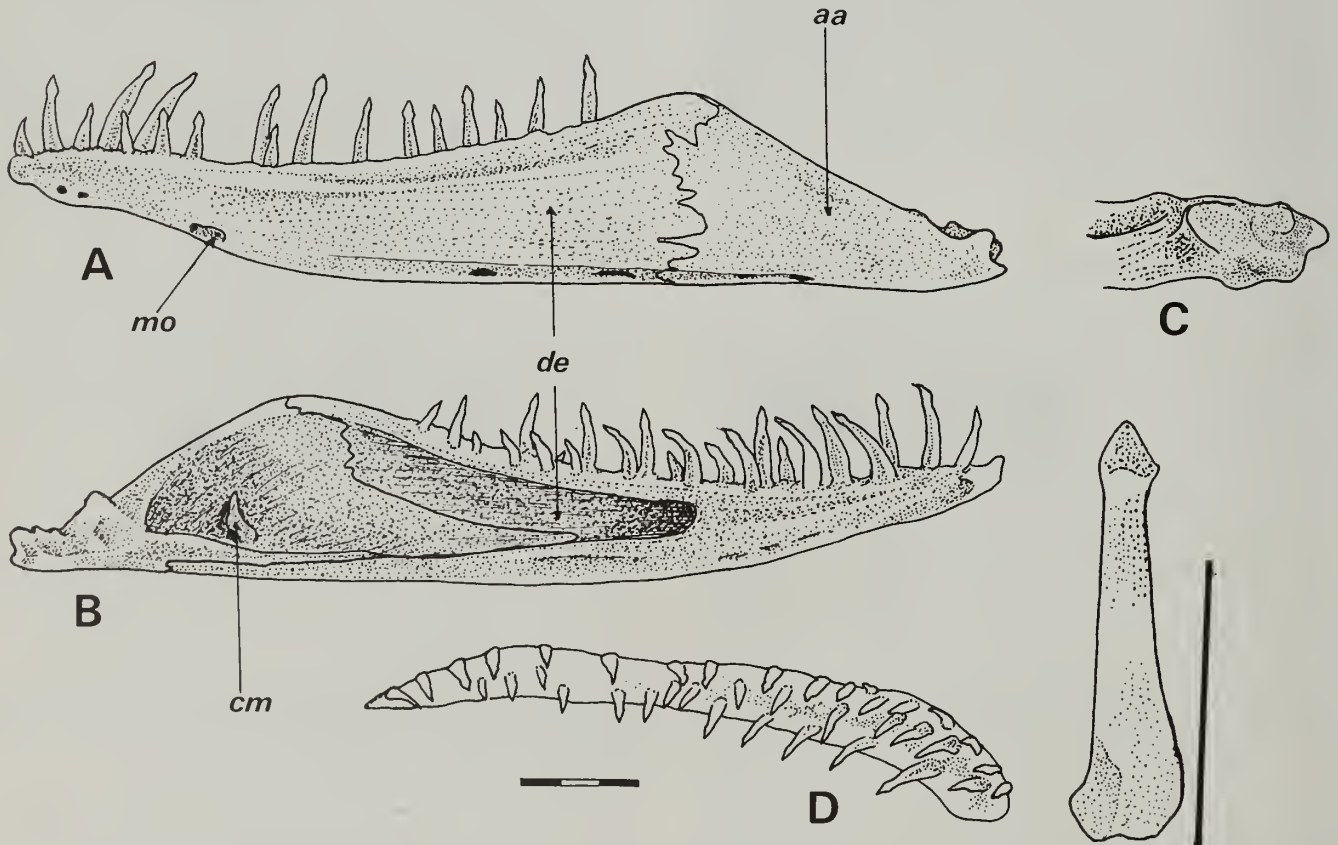

Fig. 15 *Belodontichthys dinema*: lower jaw (left) in A, lateral and B, medial views; C, dorsal view of articular surface. D, dentary tooth patch in dorsal view (LILI 89008, 89002); an isolated tooth is shown at the right.

The quadrate of *Belodontichthys* differs from that of other silurids in the form of its articular condyle (Fig. 17A). The condyle has two distinct articulatory surfaces which are deeply divided. In cross-section the entire condyle is triangular and has a slightly concave medial face. In other silurids there is a single, transverse articulatory surface which may bear a slight central indentation and which, in cross-section, is oblong with a straight or convex medial face (Figs 17B–F). The more complex articular surface of the *Belodontichthys* quadrate is correlated with the similarly complex articular arrangement of the lower jaw (see above).

Two other marked modifications of the quadrate occur within the Siluridae. In *Wallago attu*, the quadrate is deeply divided anteriorly in its saggital plane, the inner lamina contacting the posterior pterygoid and the hyomandibular dorsally, the outer lamina contacting the lateral laminate crest of the hyomandibular (Joseph, 1958; Fig. 17E). In effect, the division of the quadrate is a result of the ventral continuation of the LAP hyomandibular crest (see above). The precursor of this condition is evident in *Wallago leeri* and *Silurus asotus* where there is a prominent lateral process of the quadrate in line with that of the hyomandibular (Figs 17C, D). In *Silurus glanis* the process is present but weakly developed; it also appears to be present in *S. aristotelis* and *S. microdorsalis* but is absent in *S. torrentis* and *S. cochinchinensis* (Kobayakawa, 1989). The second derived

feature of the quadrate occurs in some *Kryptopterus* species where the anteroventral part of the bone is perforated by a large foramen (Fig. 17B). No vessel passes through the aperture and it probably acts as an expansion cavity for the adductor musculature. The foramen is present in *K. bleekeri* and *K. apogon* but not in any other *Kryptopterus* examined. A similar, but smaller foramen also occurs in *Wallago attu*. *Ompok bimaculatus* and *Hemisilurus heterorynchus* (Figs 17E, F). The ventromedial surface of the quadrate, posterior to the articular condyle is excavated by a deep fossa in most Siluridae, and it would seem that further attrition of the outer wall could lead to the development of the foramen in these taxa. The presence of a fossa or foramen in the anterior ventral part of the quadrate is not an unusual feature in siluroids and the size of the fossa is correlated with that of the dorsal process of the anguloarticular which it accommodates.

In the Siluridae the palatine is a small hoof-shaped nodular element which, in *Belodontichthys* and *Ompok* is reduced by thinning to a helmet-like element (Fig. 13).

The maxilla articulates with the anteroventral surface of the palatine. As a consequence of the orientation of the palatine against the articular facet of the lateral ethmoid, the maxilla comes to lie in a sagittal rather than transverse plane (Fig. 13D). In no other siluroid is the palatine reduced to the extent of that in the Siluridae, but the similar shape, manner of articulation and overall reduction in size of the palatine in
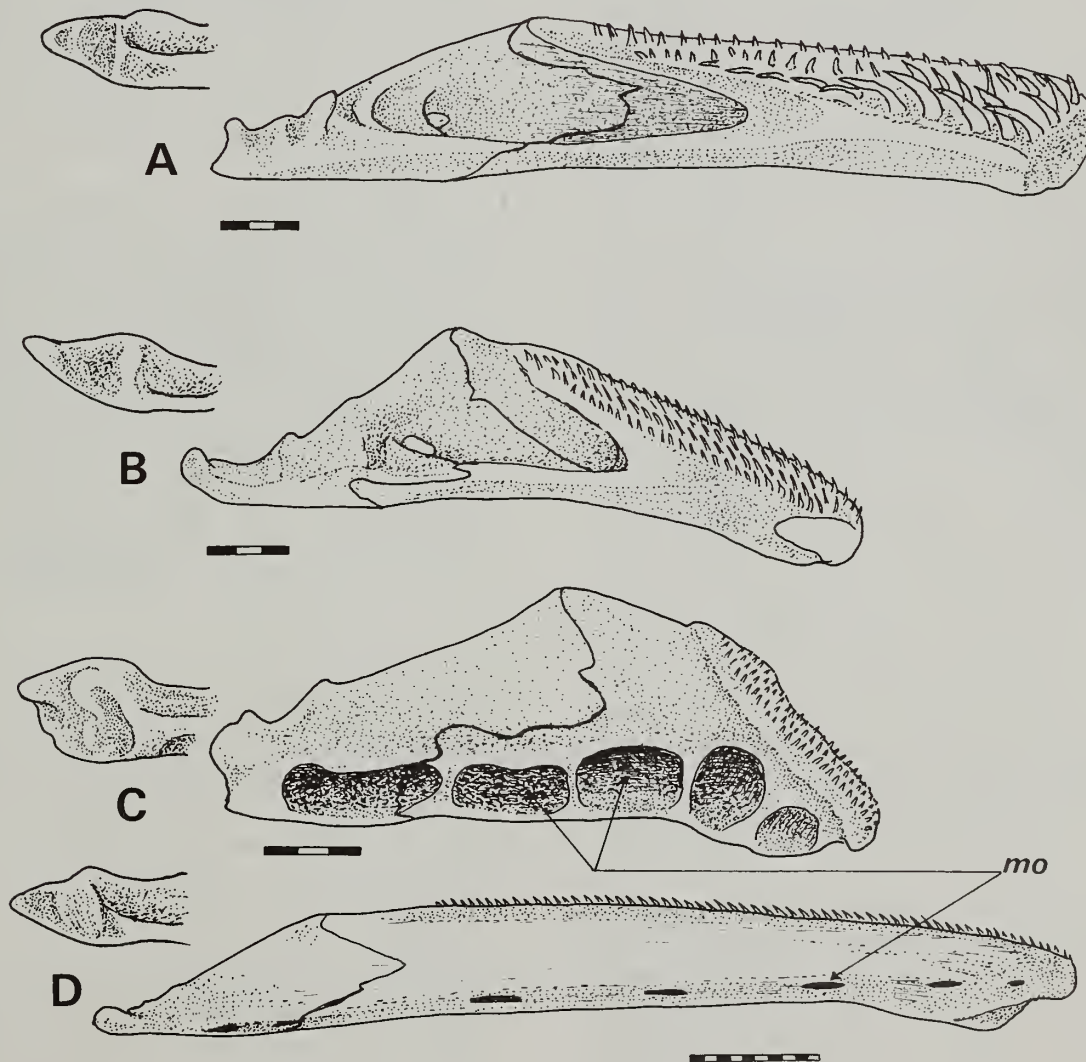

Fig. 16 Lower jaws of A, *Ompok bimaculatus*, medial view (BMNH 1891.11.20:171–8); B, *Kryptopterus bleekeri*, medial view (LILI 89030); C, *Hemisilurus heterorhynchus*, lateral view (BMNH 1982.3.29:161–2); D, *Wallago attu*, lateral view (BMNH Uncat.). The articular surfaces are shown at the left of each respective jaw.
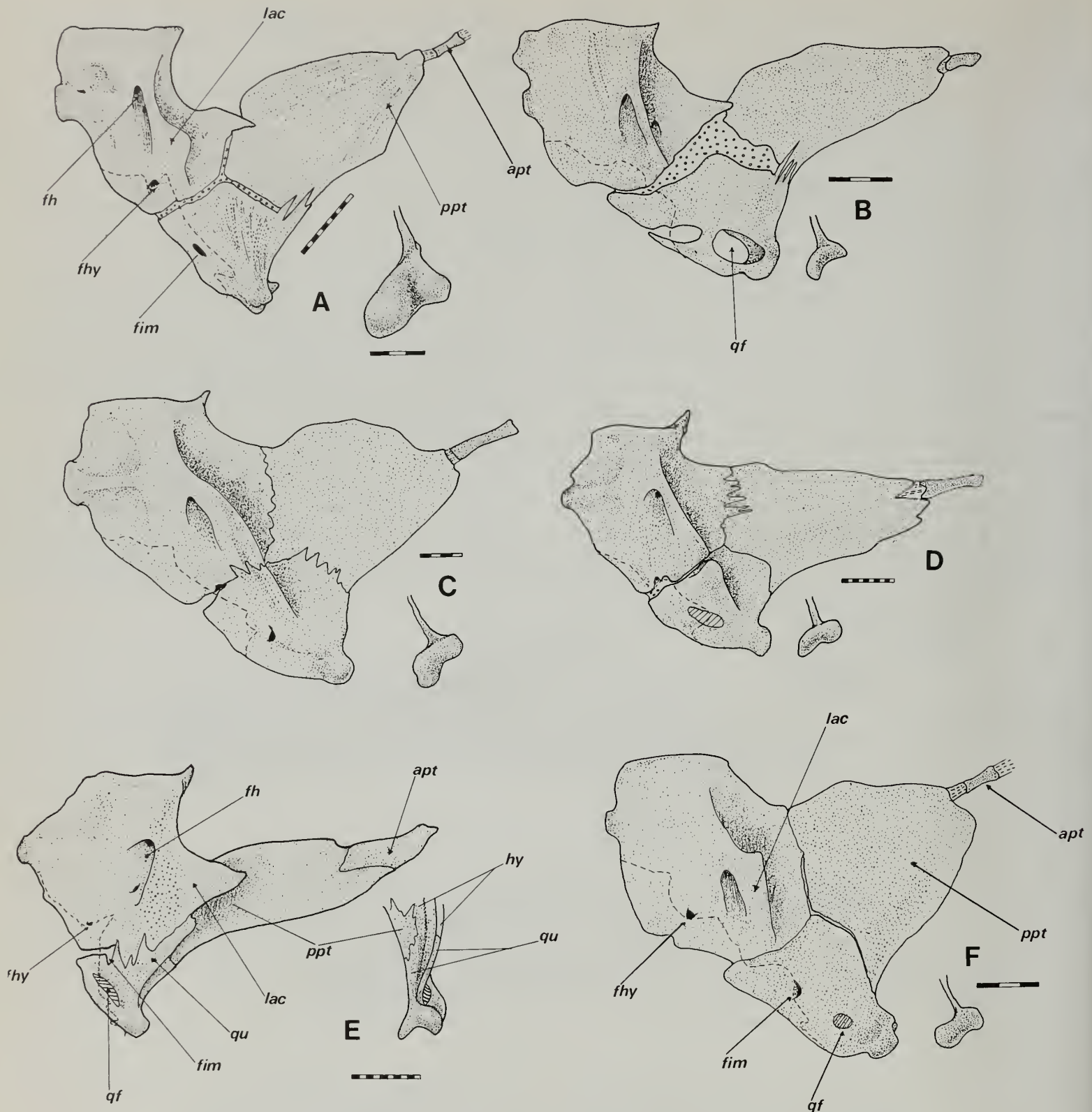
Fig. 17 Hyomandibular and palatoquadrate of A, *Belodontichthys dinema* (LILI 89008); B, *Kryptopterus bleekeri* (LILI 89030); D, *Silurus asotus* (BMNH 1880.4.21:203; E, *Wallago attu* (BMNH Uncat.), F, *Ompok bimaculatus* (BMNH 1891.11.20:171–8); all in lateral view. The articular surface of the quadrate, as viewed anteriorly, is shown to the right; the dashed lines crossing the posterior margins of the hyomandibular and quadrate indicate the anterior margin of the preoperculum when in place.

Malapteruridae caused Howes (1985) to regard the condition as synapomorphic for the two families. Bornbusch (1990) has demonstrated the non-homologous nature of the silurid and malapterurid palatine reductions and we follow him in regarding the reduced, nodular element of the Siluridae as synapomorphic for the family. The palatine in the Siluridae appears to be a single ossification and is considered as an autopalatine; in other siluroids, the posterior extension of the bone is probably the dermopalatine.

Myology (Figs 18–26)

The *adductor mandibulae* is an extensive muscle covering the entire postorbital region, its fibres separated dorsally by the *levator arcus palatini* into lateral and medial elements (Fig. 18). Posteriorly, the lateral element stems from the rim of the preoperculum and the posterolateral face of the hyomandibular, and dorsally from a long pterotic fossa (Fig. 5); its insertion is on the outer rim of the anguloarticular. The

lower part of the lateral element originates from the ventral region of the hyomandibular and quadrate; these fibres insert on an aponeurosis medial to the anguloarticular. From this aponeurosis the mandibularis section of the adductor (Aw) extends to fill the deep mentomeckelian cavity of the dentary. The medial element of the *adductor mandibulae* extends from the lower, anterior region of the hyomandibular and the posterior pterygoid bone. From there its fibres run ventro-laterally to insert aponeurotically with the outer element medial to the anguloarticular. The mandibularis branch of the trigemino-facialis nerve runs vertically across the face of the inner element, identifying the latter as the A2 division (Howes, 1983*b*).

Anteriorly, two large triangular muscles originate from the anterior pterygoid element. The lower inserts principally (and musculously) on the dorsoanterior border of the premaxilla, but a small dorsal bundle of fibres inserts tendinously onto the base of the maxilla. The upper element, whose fibres inter-mesh at their origin with those of the *adductor arcus palatini*, inserts partially on the small, helmet-shaped palatine and partially on the base of the maxilla. The upper element is identified as an *extensor tentaculi*, the lower as a *retractor tentaculi* (Figs 18, 19).

The *adductor arcus palatini* is a well-developed muscle extending the length of the parasphenoid and inserting along the medial margin of the pterygoid series (Fig. 19). Posteriorly, the muscle thickens, extends onto the lower part of the prootic and inserts broadly across the medial face of the hyomandibular; this segment is the *adductor hyomandibularis*.

The *levator arcus palatini* muscle (LAP) is a large, pyramidical element originating from the sphenotic, its fibres inserting *via* a thick tendon onto a laminar process rising vertically from the anterior rim of the hyomandibular (Figs 18, 19).

The *dilatator operculi* (DO) is an extensive, bipinnate muscle. Its anterior fibres originate from the lateral ethmoid; the main body of the muscle from the frontal, and its posterior fibres from the sphenotic. The lateral fibres run towards the central tendon at a 45° angle whereas the medial fibres lie almost parallel to the tendon. Since the frontal is deeply concave the DO lies almost vertically with the lateral and medial fibres orientated dorsally and ventrally to the central tendon. The muscle crosses the face of the LAP, passing behind the outer layer of the adductor mandibulae and the dorsal tip of the preoperculum to insert on the anterodorsal process of the operculum (Figs 18, 19).

Both the *levator* and *adductor operculari* muscles are small, triangular elements having their origins, respectively, from the ventrolateral rim and ventral surface of the pterotic. Their insertion is across the upper medial face of the operculum, that of the adductor overlapping the posterior half of the levator (Fig. 18).

The *epaxialis* muscle extends as far forward as the anterior margins of the frontals (Figs 20, 21). Above the cranium, the muscle is a single mass undivided by a medial septum or containing any myocommata. Only posteriorly, behind the supraoccipital, does the muscle become divided in the midline by the septum stretching from that bone to the 1st neural spine.

Comparisons

Among other silurids, the *adductor mandibulae* morphology of *Belodontichthys* most closely resembles that of *Ompok*,

Wallago and *Silurus* (Figs 20, 21). In all these taxa the outer element (A1) is extensive, almost square-shaped, with a near vertical anterior border and straight dorsal border. The posterior origin of the muscle is from the supra- and pre-opercular bones, and its dorsal origin from the margin of the pterotic, in common with other silurids. In contrast, however, the pterotic margin is hidden, the lateral fibres of the epaxial muscle appearing contiguous with those of the *adductor*. The fibres of the inner element (A2) run ventrolaterally and almost vertically to their lower jaw insertion. The eye lies immediately lateral to A2.

In *Kryptopterus* (Figs 22, 24B) and *Hemisilurus* (Fig. 23) muscle A1 has a concave anterior border and a short dorsal origin from the pterotic, the margin of which visibly separates the epaxial from the adductor musculature. In *Kryptopterus bleekeri*, *K. apogon*, *K. moorei*, *K. limpok* and *K. cryptopterus*, the eye lies lateral to muscle A1 and the area of the muscle behind the eyeball is entirely tendinous. That tendinous sheet also provides a fascia for the fibres of muscle A2 which runs ventroanteriorly and obliquely to their lower jaw insertion. In *K. bicirrhis*, the muscle A1 is narrow crescent with only a few fibres inserting on the dorsal rim of the anguloarticular (Fig. 24A). The remainder of the muscle extends forward onto the lower jaw without the intervention of an aponeurosis to become continuous with Aw.

The arrangement of the *adductor mandibulae* musculature in the Siluridae is rather typical of that in the majority of siluroids; the insertion of the outer element on both dorsal and medial aspects of the anguloarticular is a plesiomorphic arrangement (Howes, 1983*a*). However, the tendinous region behind the eye in some *Kryptopterus* species is an unusual feature paralleled in the Hypophthalmidae (Howes, 1983*a*). The vertical orientation of the fibres of A2 in *Belodontichthys*, *Ompok*, *Silurus* and *Wallago* is also unusual but a similar situation is present in the schilbeid *Eutropiichthys* where the fibres run not only vertically but turn posteriorly to join a central tendon of the muscle (Fig. 25). In *Eutropiichthys* muscle A2 has a uniquely derived feature whereby it originates from the lateral ethmoid as well as the frontal and sphenotic and skirts the dorsal curvature of the eyeball (Fig. 24A).

In all Siluridae both *extensor* and *retractor tentaculi* muscles are present (Bornbusch, 1990). As in *Belodontichthys*, the extensor in other silurids is an elongate muscle, its anterior portion running obliquely from the lateral ethmoid to the palatine; its posterolateral portion extending from the orbital region. In *Kryptopterus bicirrhis* the extensor runs from the dorsal rim of the pterygoid whereas in other *Kryptopterus* it originates from the cranium, usually the orbitosphenoid, its fibres extending from a thin fascia covering the *adductor arcus palatini* (cf Figs 24A, B). In *K. apogon*, *K. bleekeri* and *K. limpok* the muscle fibres extend from the medial surface of the frontal (Fig. 23B) and in *Silurichthys*, the origin of the extensor covers the entire orbital face of the cranium (orbitosphenoid, pterosphenoid and prootic). In all silurids there is a dual palatine insertion of the *extensor*. Those fibres running from the lateral ethmoid inserting on the palatine's dorsal surface and lateral rim, while those extending horizontally from the orbital region insert on the bone's ventral surface and medial rim (Fig. 21B).

When present in other siluroids the *extensor tentaculi* originates principally from the lateral ethmoid and orbito-sphenoid, the fibres being orientated from postero- to antero-laterally and often broadly inserting along the length of the palatine (in the majority of siluroids, the palatine is a
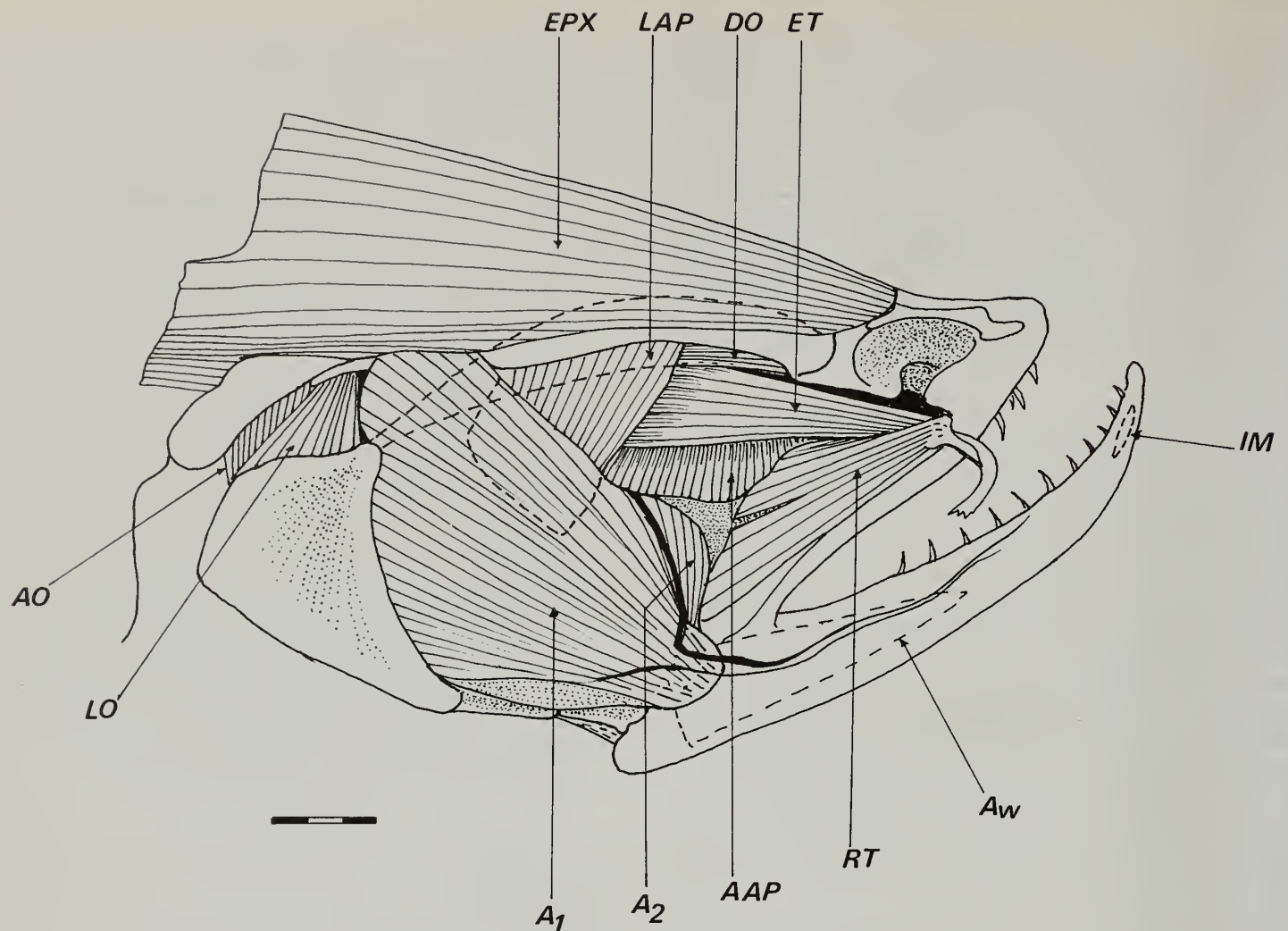
Fig. 18   *Belodontichthys dinema*: superficial cranial musculature; dashed lines indicate the underlying DO and LAP muscles (LILI 89002).

long, rod-shaped bone, unlike the nodular element of the Siluridae). Among other siluroids examined, only in Hypophthalmidae does the *extensor* run longitudinally from the rear of the orbit. In this case, however, the muscle originates from the body of the *adductor arcus palatini* along the dorsal border of the posterior pterygoid, whereas in silurids its origin covers a broad area of the posterior part of the *adductor arcus palatini* and encroaches on the parasphenoid, orbitosphenoid, pterosphenoid and, in *Wallago*, also on the sphenotic.

In most other silurids the *retractor tentaculi* originates from a connective tissue fascia covering the posterior pterygoid medial to muscle A2. In *Wallago*, as in *Belodontichthys* there are two distinct segments of the retractor, the upper of which inserts on the base of the barbel, the lower passing beneath the upper segment to insert at the midpoint of the maxilla (Fig. 21C). Only in *Kryptopterus cryptopterus* is there a connection of the extensor with the premaxilla as in *Belodontichthys*. *Belodontichthys* most closely resembles *Kryptopterus bicirrhis* in its relatively short retractor and in the muscle's origin from the anterior pterygoid. Bornbusch (1990) has pointed out that the length and orientation of the *retractor tentaculi* in most Siluridae is a probable correlate of the shortened palatine.

The distribution of a *retractor tentaculi* amongst siluroids has not been documented. Howes (1983a) drawing on a limited survey of Old and New World taxa, supposed that the muscle had been derived independently in several lineages. No evidence has emerged from this study to alter that opinion.

In all of the Siluridae, the *levator arcus palatini* (LAP) is extensive, originating from the sphenotic and (with the exception of *Kryptopterus bicirrhis*) from the posterior margin of the lateral ethmoid. The LAP inserts on the anterior margin of the hyomandibular and in *Ompok* and *Wallago*, as in *Belodontichthys*, the insertion area is a laminar projection of the bone (Fig. 17A). A large LAP is commonly encountered among siluroids (Howes, 1985), and is also present in the Diplomystidae.

In nearly all silurids the *dilatator operculi* (DO) is elongate and extends well forward onto the underside of the sphenotic and frontal. *Belodontichthys* shares with *Ompok*, *Wallago* and *Silurus* a lateral ethmoid origin of the muscle. In *Kryptopterus bicirrhis* and *Silurichthys* the DO is confined to the postorbital part of the cranium and its origin involves only the lateral part of the sphenotic. In *K. cryptopterus* and *K. limpok* the muscle originates further forward, from the orbital part of the sphenotic and in *K. apogon* and *K. bleekeri* from the frontal as well (Fig. 22B). In the two latter species, the DO lies flat against the underside of the frontal and the orbital portion of the sphenotic. It then turns abruptly into the vertical plane where it passes medial to the LAP. At this point, the lateral edge of the muscle is firmly attached to the sphenotic border by a tendon thus seemingly allowing only the medial aspect of the muscle free movement.

The morphology of the DO among siluroids is variable and that encountered in the Siluridae is not unusual. An elongate DO extending over the ventral surfaces of the frontal and sphenotic is a common condition amongst the Pimelodidae, Bagridae, Clariidae and Loricarioidei (Howes, 1983a), and a
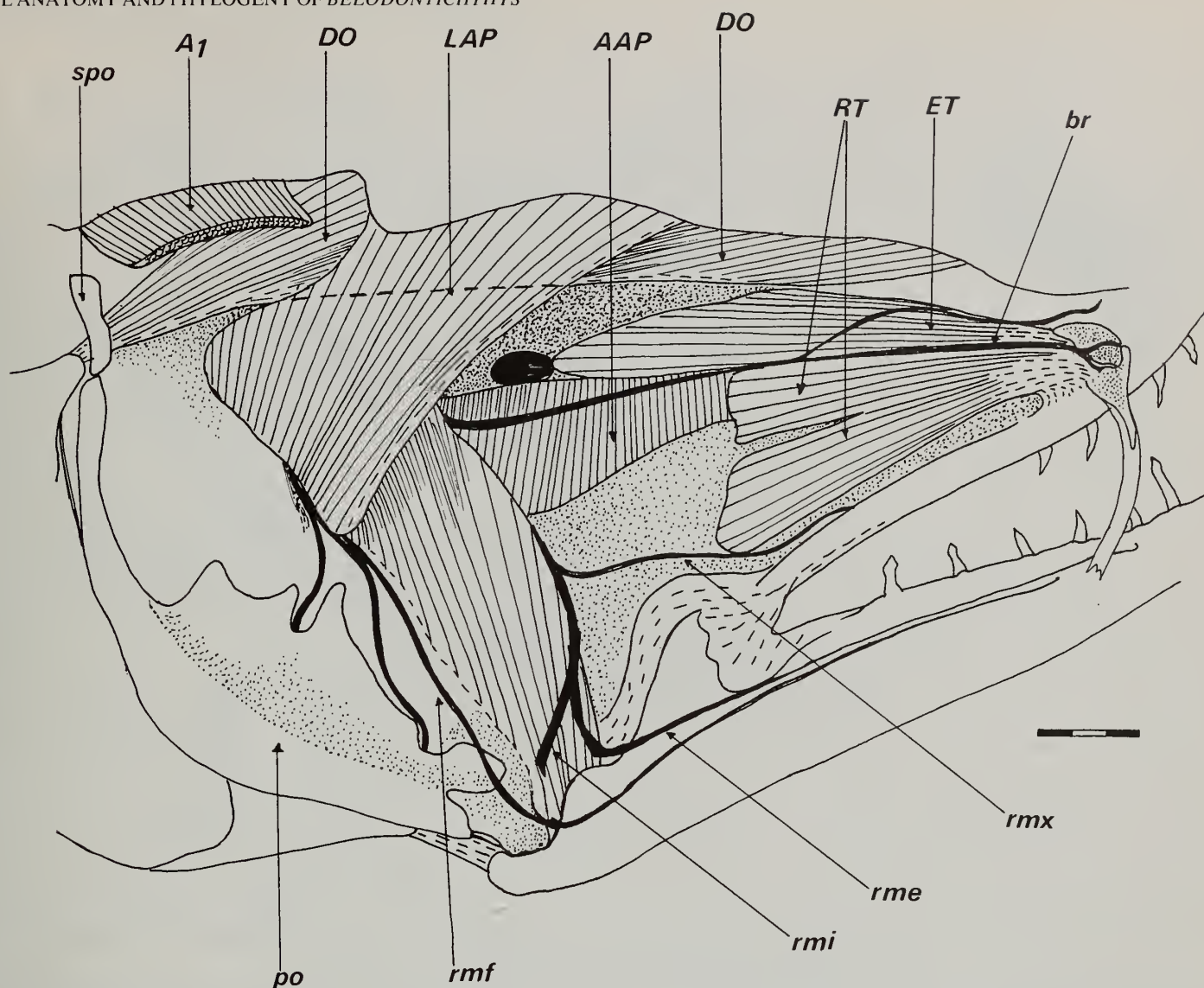
Fig. 19 *Belodontichthys dinema*: deeper cranial musculature. Muscle A1 is cut through; the lower border of DO is indicated by dashed line crossing LAP (LILI 89008).

large DO with a frontal origin occurs in the Diplomystidae. The presumed plesiomorphic condition of the DO (that which is regularly encountered in other ostariophysans) is present in *Ictalurus* where the muscle is small and vertically orientated, with its origin confined to the posteroventral region of the sphenotic.

The *adductor arcus palatini* (AAP) has a variable morphology in the Siluridae. The usual condition is for the muscle to run between the parasphenoid and the pterygoid bones, while posteriorly it covers the lower part of the medial face of the hyomandibular and is considered a separate element, *viz* the *adductor hyomandibularis* (Winterbottom, 1974). This condition occurs in *Belodontichthys, Hemisilurus, Silurus, Wallago, Silurichthys, Hito, Ompok, Kryptopterus bicirrhis, K. cryptopterus, K. limpok* and *K. moorei*. In contrast, in *K. bleekeri* and *K. apogon*, the AAP extends dorsally to cover the orbitosphenoid, pterosphenoid and medial part of the frontal. Only in Schilbeidae (*Schilbe*) where the AAP attaches to the frontal (Fig. 26) have we encountered a condition similar to that in the two cited *Kryptopterus* species.

In the other members of the Siluridae examined the epaxial musculature extends forward onto the frontal in *Silurus, Wallago, Ompok* and *Hemisilurus*. However, only in *Wallago* and *Ompok* does the musculature cover a large posterior area of the bone. In *Silurus* only a small region of the bone is covered and the anterior border of the muscle is marked by a strong transverse frontal ridge. *Hemisilurus* lacks the frontal concavity

of the former taxa, the frontal being convex with the epaxial muscle inserting, as in *Silurus*, along a prominent frontal ridge. Like *Belodontichthys*, the supraoccipital crest in *Ompok* is reduced in height and does not divide the muscle bloc whereas in other silurids the muscle is divided in the midline by the crest.

In siluroids, the mandibularis branch of the trigeminal nerve usually follows a course across the junction of muscle A1 with the lower jaw (often penetrating through dense connective tissue), passes ventrally across the posterolateral face of the anguloarticular and then anteriorly along the sensory groove of the dentary to innervate the labial tissue. Along this latter part of its course the nerve is joined by the external branch of the hyomandibular nerve trunk which leaves the lower hyomandibular foramen and passes anteroventrally between muscles A1 and A2 then laterally across the mandibuloquadrate joint to run along the outer face of the lower jaw. This nerve pattern has been found in all the siluroids examined.

DISCUSSION

Derived characters shared by *Belodontichthys* with other Siluridae

In the preceding comparative analyses we have identified a number of derived characters possessed by *Belodontichthys*
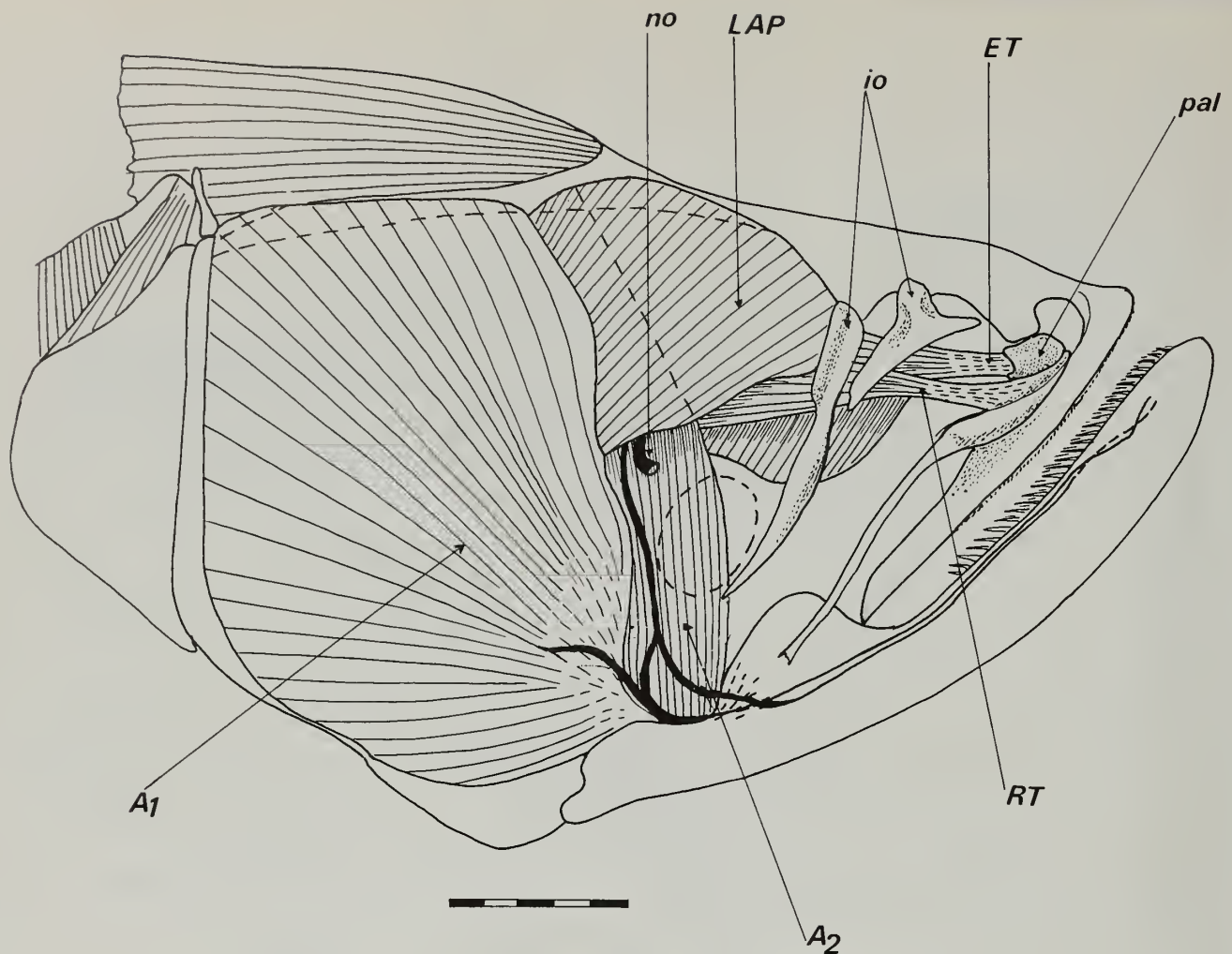
Fig. 20 *Ompok bimaculatus*: cranial musculature. Dashed lines indicate underlying DO and A2 muscles. The circular dashed line covering A2 muscle indicates the position of the eye (BMNH 1891.11.20:171–8).

and shared with other genera of the Siluridae. The mono-phyletic nature of the Siluridae has been shown by Bornbusch (1990) who recognises five synapomorphies. These are the reduced palatine; the occlusion of the frontal margin by the lateral ethmoid and sphenotic; the compression of the transcapular ligament of the posttemporosupracleithrum and the absence of dorsal fin radials and posterodorsally shifted anal fin pterygiophores. In addition to these synapomorphies we recognise a further three, *viz*; the modification of the frontal sensory canal system (p. 140); the vertical LAP crest on hyomandibular and the longitudinally aligned *extensor tentaculi* muscle.

In addition to these basic silurid synapomorphies *Belodontichthys* possesses the following derived features with;

All Siluridae apart from *Silurus*:

1. Occipital canals elevated (p. 141)
2. Exoccipital contributes to cranial roof; vagus foramen re-located to posterior face (p. 141)
3. Dorsoanterior process of hyomandibular reduced or absent (p. 145; discussed in Bornbusch, 1988)

Exclusively with *Silurus, Wallago* and *Ompok*;

4. Raised lateral border of pterotic (p. 140)
5. Muscle A2 aligned vertically to jaw insertion (p. 149)
6. *Dilatator operculi* originating from the lateral ethmoid (p. 150)
7. Lateral parasphenoid shelf meeting similar pterosphenoid shelf (p. 140; see also Character 20)

8. Continuous row of long, recurved inner teeth in both jaws (p. 142)
9. Partially excavated frontals covered posteriorly with epaxial muscle (p. 139)

Exclusively with *Wallago* and *Ompok*;

10. Upwardly angled vomer and ethmoid (p. 139)
11. Thick, blunt ethmoid cornua (p. 138)
12. Reduced anterior fontanelle (p. 139)
13. Lateral branch of frontal sensory canal transversely or posteriorly directed (p. 140)
14. Expansion of ventral part of LAP hyomandibular crest (p. 145)

Exclusively with *Ompok*;

15. Parasphenoid angled upward relative to vertebral axis, its posterior part bearing a prominent keel (pp. 140)
16. Prominent frontal crests enclosing anterior and posterior fontanels (p. 139)
17. Raised border of pterotic (p. 140)
18. Reduced vomerine tooth patches, teeth supported on bony laminae or pedestels (p. 139)
19. Ventrally situated palatine articulatory facet on lateral ethmoid (p. 139)
20. Deep indentation of pterosphenoid–prootic junction and shelflike extension of optic nerve foramen (p. 140)
21. High and transversely aligned premaxillary ascending process (p. 143)
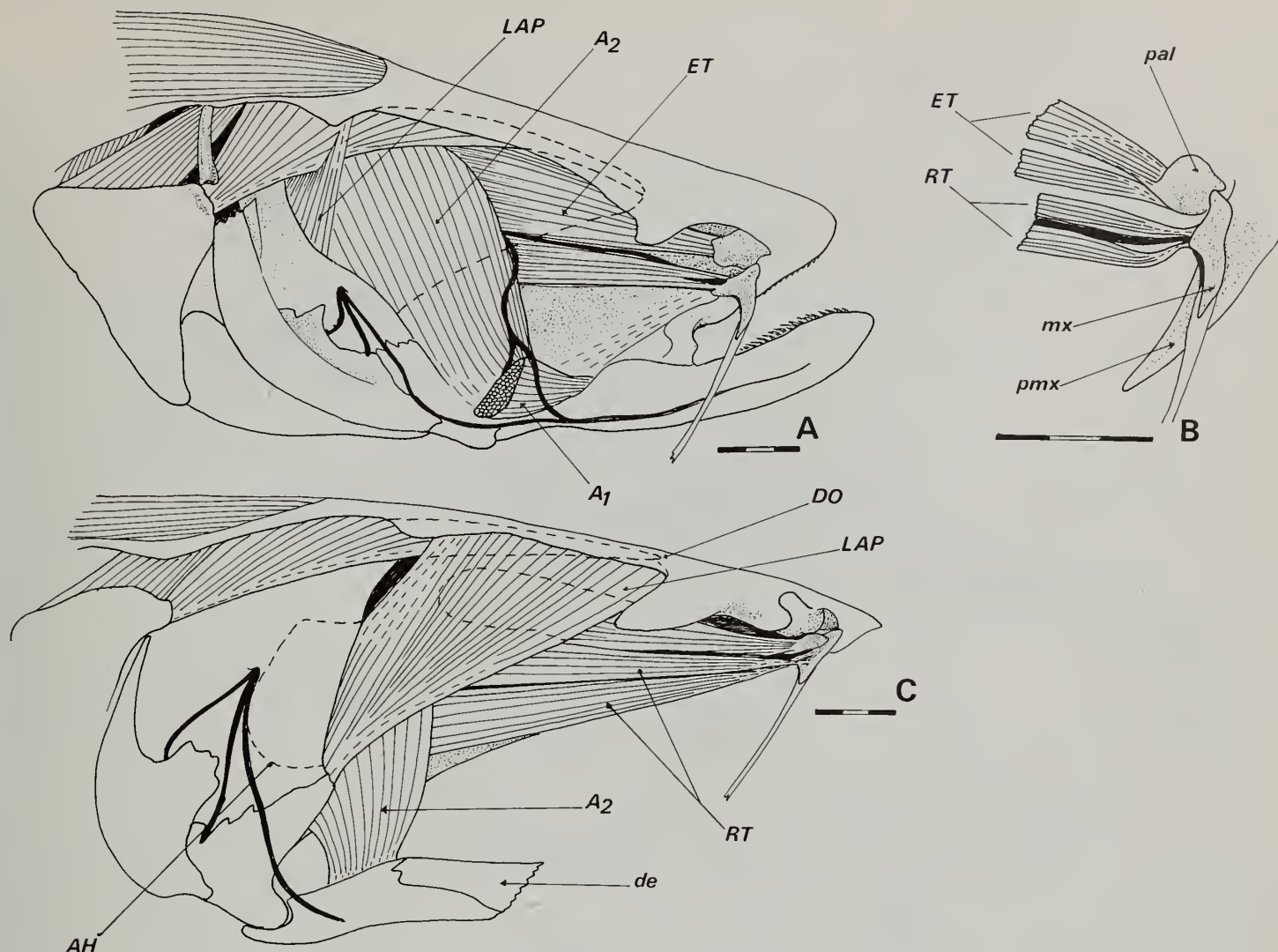22. Helmet-shaped palatine (p. 147)

Fig. 21 A, *Silurus triostegus*: deep cranial musculature; most of muscles A1 and LAP removed; dashed lines indicate extent of DO and LAP; B, detail of insertion of ET and RT muscles (BMNH 1969.3.3:168–76); C, *Wallago attu*: deep cranial musculature; posterior border of the medial AH indicated by dashed lines on hyomandibular (BMNH 1891.11.30:156–61).

23. Dorsal margin of A1 portion of *adductor mandibulae* muscle contiguous with *epaxialis* musculature (p. 149)

Exclusively with *Kryptopterus bleekeri* and *K. apogon*;

Arrow-shaped tooth tips. This character has been discussed above (p. 143) and is interpreted as homoplastic in the light of its incongruent relative to the above listed synapomorphies.

Exclusively with *Kryptopterus* and *Hemisilurus* and some *Silurus* species;

Accessory foramen in prootic for hyomandibular branch of trigeminal nerve. This feature is difficult to evaluate as a synapomorphy linking these taxa with *Belodontichthys* since it occurs sporadically in *Silurus*. Its absence in other silurids must therefore be considered either as a derived loss or independently derived in *Belodontichthys*, some *Silurus* species, *Kryptopterus* and *Hemisilurus*; the latter situation being implied from the phylogenetic reconstruction given here (Fig. 27).

Phylogenetic interpretation

The distribution of these synapomorphies indicates *Belodontichthys* and *Ompok* as sister-taxa, forming the sister group to *Wallago* (Fig. 28). Ostensibly, through lacking three lower-level synapomorphies (Nos 1–3), *Silurus* is excluded from the main-body of Siluridae and appears as its sister-group. However, the six synapomorphies *Silurus* shares with *Wallago*, *Ompok* and *Belondontichthys* provide the more parsimonious system of relationships (Fig. 27).

The three less inclusive synapomorphies which *Silurus* lacks, namely, elevation of the semicircular canal tubes, repositioning of the vagus foramen and reduced anterodorsal process of the hyomandibular, may be viewed either as secondary loss and reacquisition or plesiomorphic retention. The first hypothesis demands that *Silurus* will have lost and regained one character (hyomandibular process) while retaining the plesiomorphic condition of the vagus foramen and semicircular canal (one loss and one gain). The other hypothesis demands that the two derived lineages would have independently acquired the vagus foramen and canal condition (two separate gains) whilst sharing the loss of the hyomandibular process with *Silurus*. In terms of losses and gains both hypotheses have equality.

In our view, we consider it anatomically more justified that *Silurus* has plesiomorphically retained these characters. In the positioning of the vagus foramen *Silurus* displays a transitional derived condition with respect to any non-silurid and the derived silurid lineages (it seems that this feature and the elevation of the semicircular canal tubes are functional correlates, the taxa with the largest vagus foramen, *Belodontichthys*, *Silurichthys* also have the tallest semicircular canal ridge). The anterodorsal process of the hyomandibular
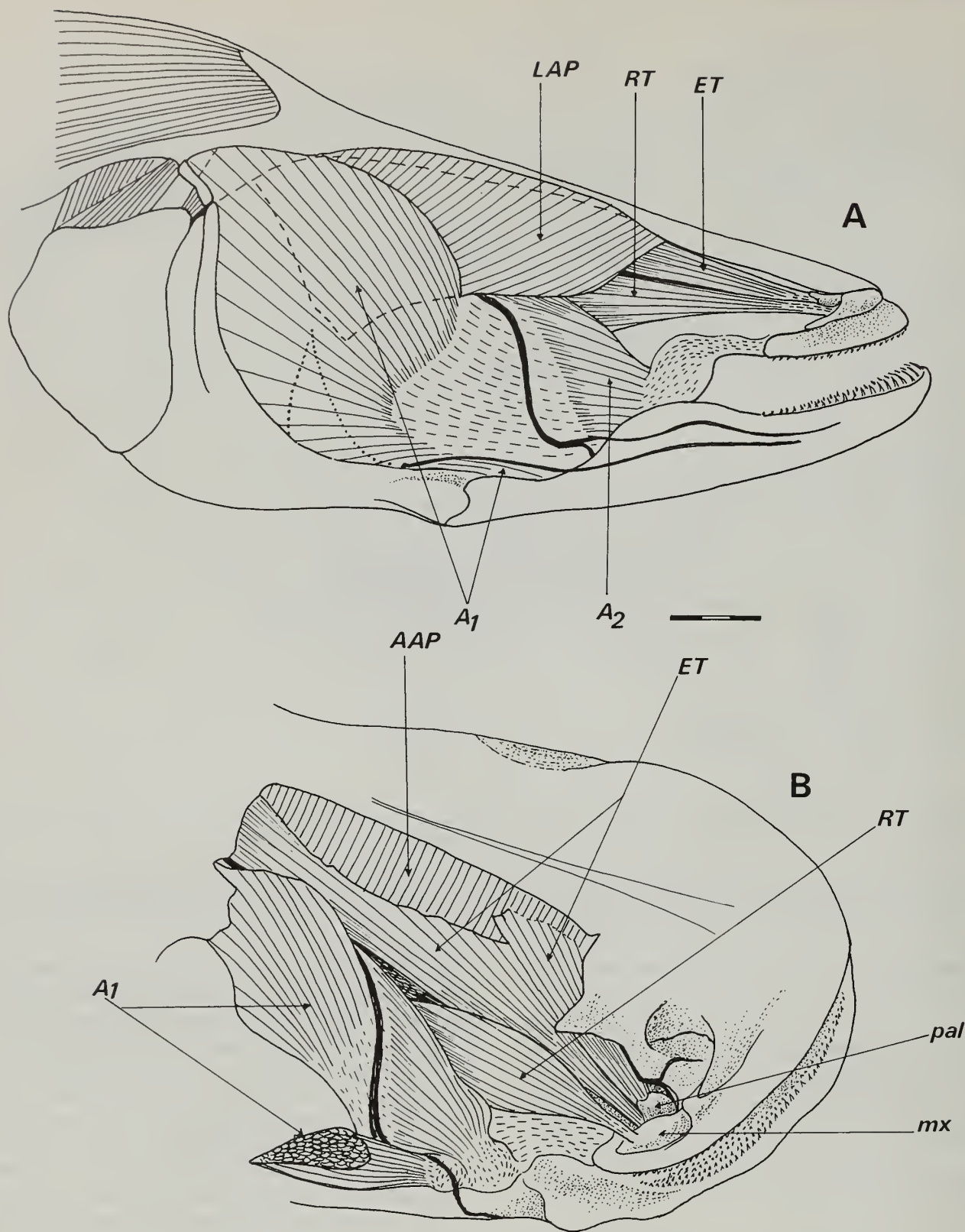
Fig. 22 *Kryptopterus bleekeri*: cranial musculature; A, lateral view with superficial part of A1 removed; dotted lines show course of hyomandibular nerves, dashed lines the outline of underlying LAP and DO muscles. B, dorsolateral view with LAP and DO muscle removed to show frontal attachment of AAP (LILI 89030).

is unlikely to have been lost and regained, since there would seem to be no functional reason to account for this pattern of events. Reasoning from an anatomical–functional viewpoint the vagus foramen-semicircular canal character should be the synapomorphy for the entire group minus *Silurus*. Identification of further synapomorphies from other anatomical complexes are needed to support one or other of these hypotheses. In this regard, Bornbusch (1988) has attempted a PAUP phylogenetic analysis involving several more characters utilized from the postcranial skeleton and has arrived at a conclusion different from ours. In his phylogeny,

Belodontichthys appears as the sister group to one embracing *Kryptopterus apogon* group + *Ceratoglanis* and *Hemisilurus; Ompok bimaculatus* and *Wallago* are far removed from this group and *Silurus* appears as the sister-group to other Siluridae. The features by which Bornbusch relates *Belodontichthys* involve barbel length, barbel supports, truncated lateral process of the lateral ethmoid and short hyomandibular anterior process.

Our working concept of *Silurus* has been restricted to the type species *S. glanis* and *S. asotus*. Kobayakawa (1989) distinguishes two monophyletic groups of *Silurus* but the
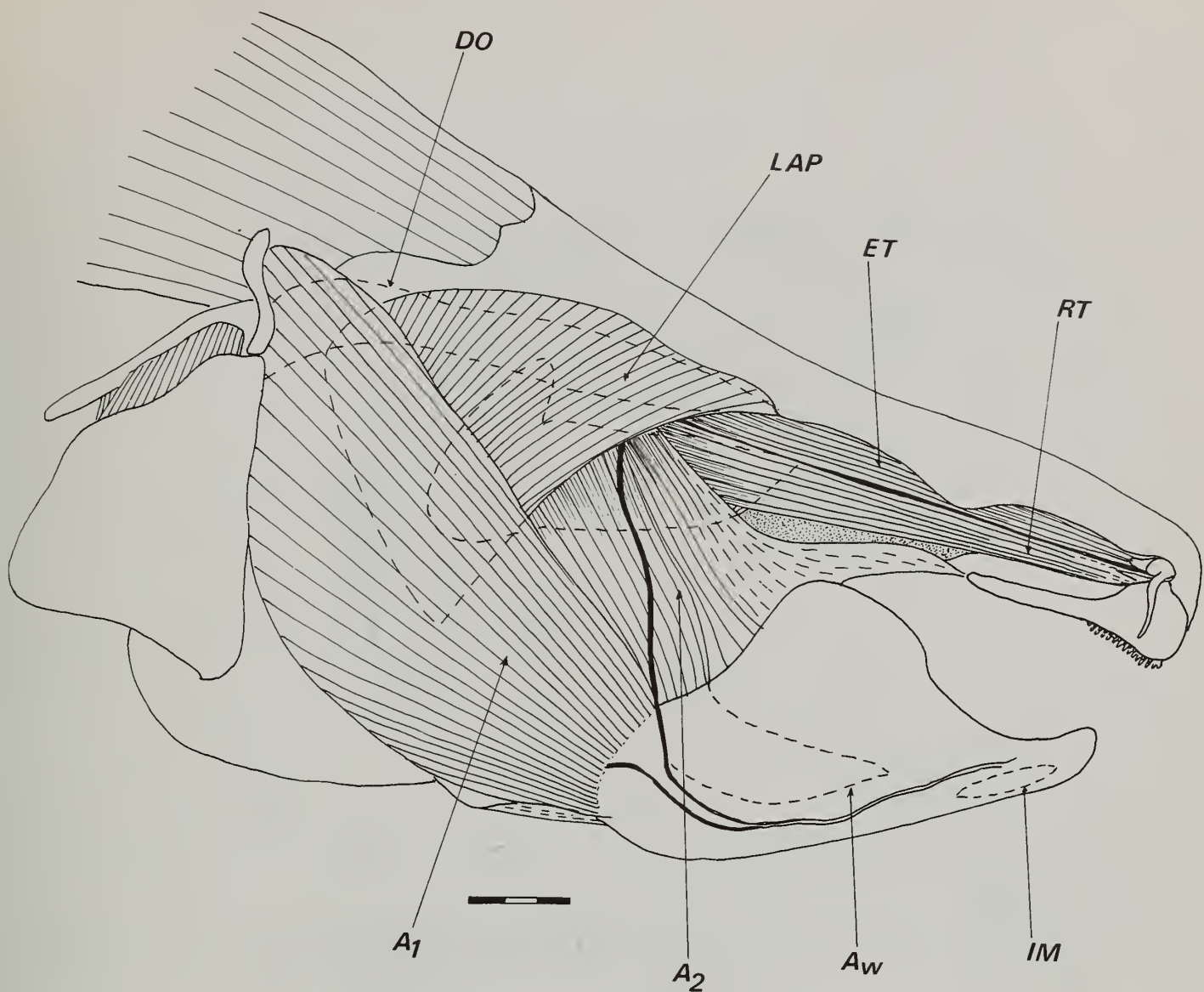
Fig. 23 *Hemisilurus heterorhynchus*: cranial musculature in lateral view; underlying AW, IM, Do, LAP and AAP muscles indicated by dashed lines (BMNH 1982.3.29:161–2).

synapomorphies she recognises as conferring monophyly on the genus appear insubstantial. Confluence of anal and caudal fins, reduced dorsal fin and rounded, truncated or emarginate caudal fin, the characters she proposes as synapomorphic for the genus, are not restricted to *Silurus* but occur elsewhere in the Siluridae and among other siluroids.

As recognised here *Ompok* includes, in addition to the type species, *O. bimaculatus, O. pabda,* and *O. liecanthus.* We have examined too few species to be sure of their generic assignment.

Our findings support those of Bornbusch (1988) that the genus *Kryptopterus* is non-monophyletic. Myological synapomorphies (orbital region of muscle A1 entirely tendinous; AAP and *retractor tentaculi* muscles extending from the medial surface of the frontal) appear to unite *K. bleekeri, K. apogon, K. cryptopterus* and *K. limpok,* species which Bornbusch (1988) grouped in two assemblages.

Hemisilurus, despite its specialized features (see Bornbusch & Lundberg, 1989) is myologically generalized and together with *Ceratoglanis* (Bornbusch & Lundberg, 1989) seems to be the sister-group to the other taxa considered. In our cladogram (Fig. 27) we have placed these and the other silurid genera (*Silurichthys* and *Hito*) together in a single unresolved lineage.

Neurocranial modifications and their evolution in *Belodontichthys*

The most outstanding feature of *Belodontichthys* compared with other Siluridae, and indeed other siluroids, is the excavation of the frontals and the occupation of the resultant space by epaxial muscle. The excavation has taken the form of a medial bowing giving a hull-like appearance to the skull roof. In addition to a change in profile, however, there has been a further modification to the anterolateral branch of the frontal sensory canal. This branch of the canal, itself a derived character of the Siluridae, is further derived in *Belodontichthys* by reversing direction to run posterolaterally (p. 140). The lateral opening of the canal retains its position above the orbit, anterior to the opening of the temporal canal with which it shares communication with the infraorbital canal. Thus, the lateral opening by virtue of its fixed position, presumably dictated early in the ontogeny of the sensory pore system, acts as a landmark from which to chart the topographical restructuring of the rest of the frontal and surrounding bones.

The posterior curvature of the lateral branch of the frontal canal is due to the anterior movement of the cross-commisure which is positionally associated with the posterior margin of
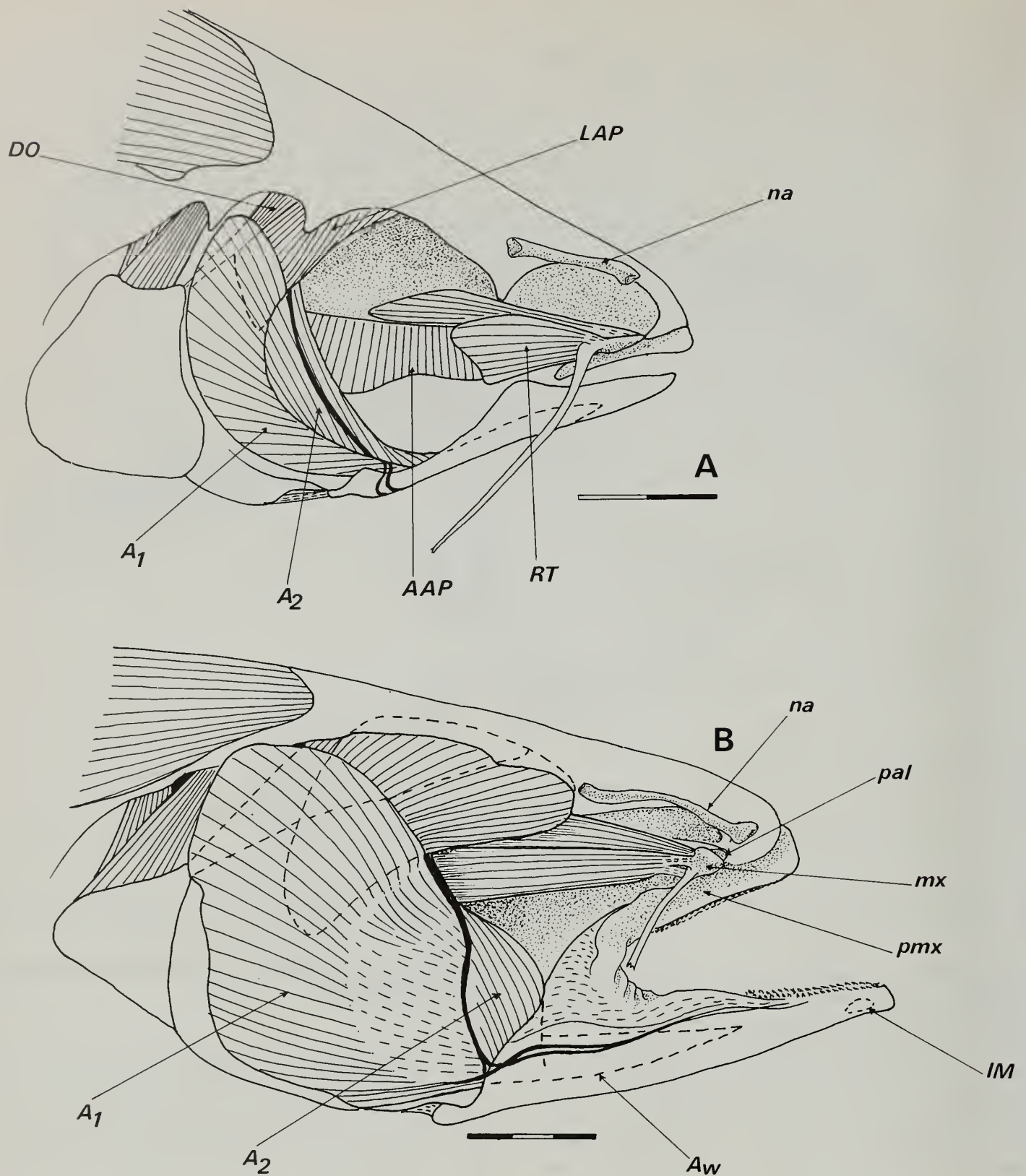
Fig. 24 A, *Kryptopterus bicirrhis* (BMNH 1982.3.29:163–7); B, *K. cryptopterus* (LILI 9009): cranial musculature in lateral view; underlying DO, LA, AW and IM muscles indicated by dashed lines.

the anterior fontanel. In *Belodontichthys* the anterior fontanel has become so shortened that it remains merely as a small opening between the frontal crests. The posterior fontanel is also reduced in size and almost obliterated by the medial crests.

The anterior relocation of the cross-commissure has given the impression of a shortened longitudinal sensory canal. However, although the anterior horizontal part of the canal is short in comparison to that in other siluroids, the remaining, posterior part of the canal has become vertically orientated owing to the medial elevation of the frontal to form a crest.

When the length of the vertical part of the canal is taken into consideration it would seem that in overall length the longitudinal canal approximates that of other Siluridae.

The posterolateral branch of the frontal canal is possibly equivalent to the side branch noted by Lundberg (1982) which communicates with the infraorbital canal in most members of the Ictaluridae. In the Ictaluridae and Diplomystidae (Lundberg, 1982; Arratia, 1987), however, there is no link between the temporal canal of the sphenotic and the infraorbital canal, whereas in Siluridae there is a tripartite connection between the temporal, frontal and
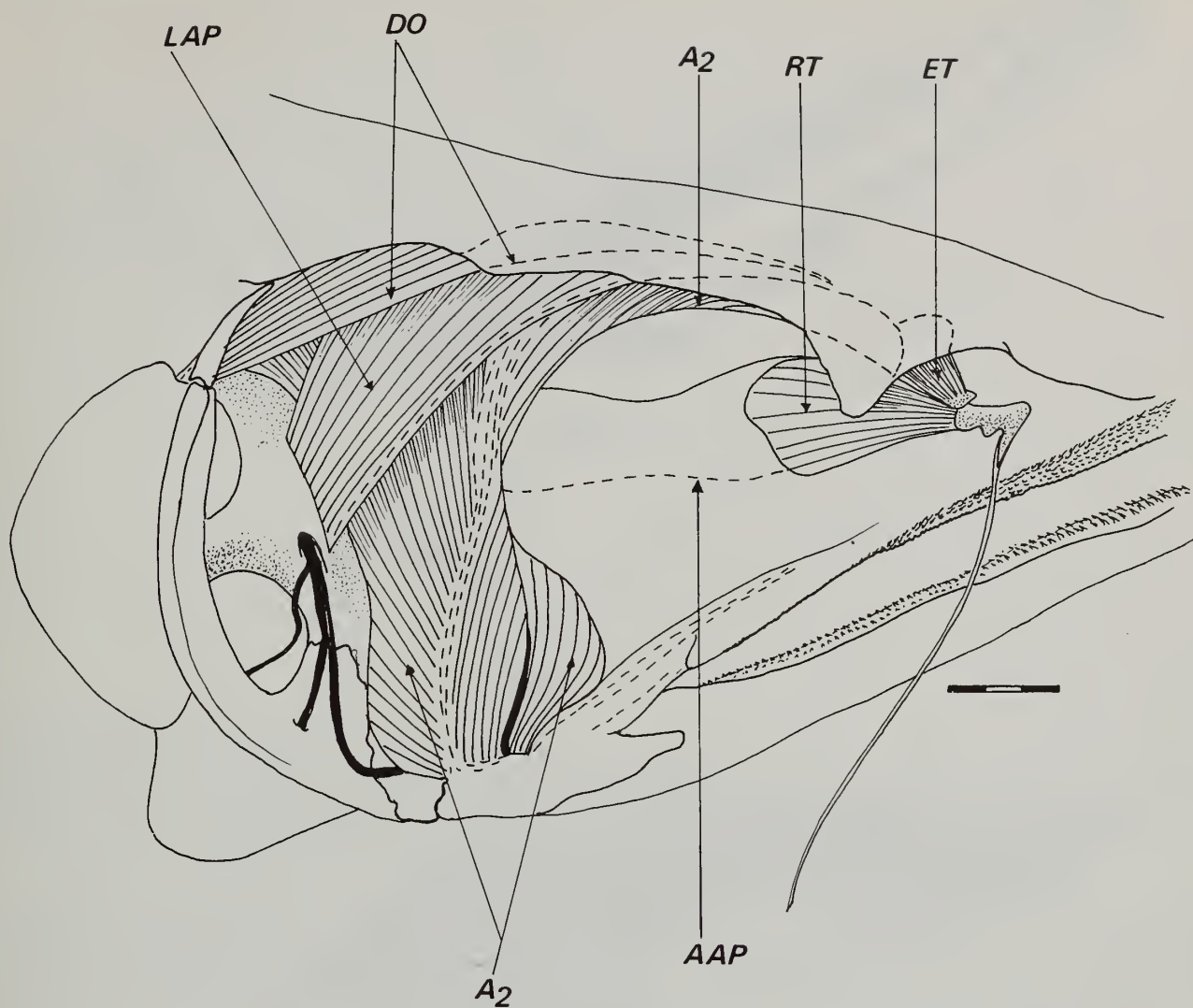
Fig. 25 *Eutropiichthys vacha*: deep cranial musculature; muscle A1 removed, underlying muscles shown by dashed lines. NB. AAP lies medial to pterygoid bones (BMNH 1891.11.30:162–9).
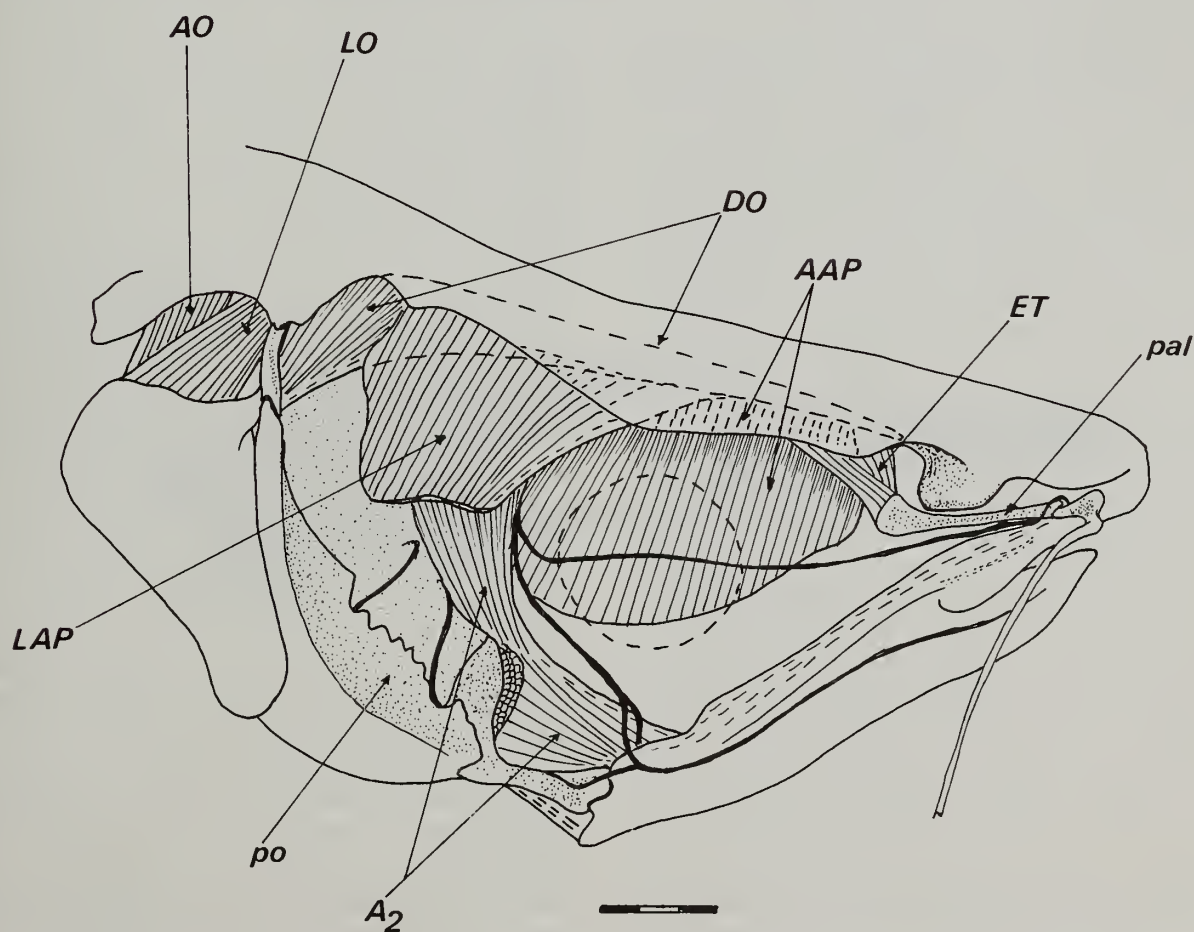

Fig. 26 *Schilbe mystus*: deep cranial musculature; muscle A1 totally, and A2 and LAP muscles partially removed; underlying muscles and position of eye indicated by dashed lines (BMNH 1982.4.13:3242).
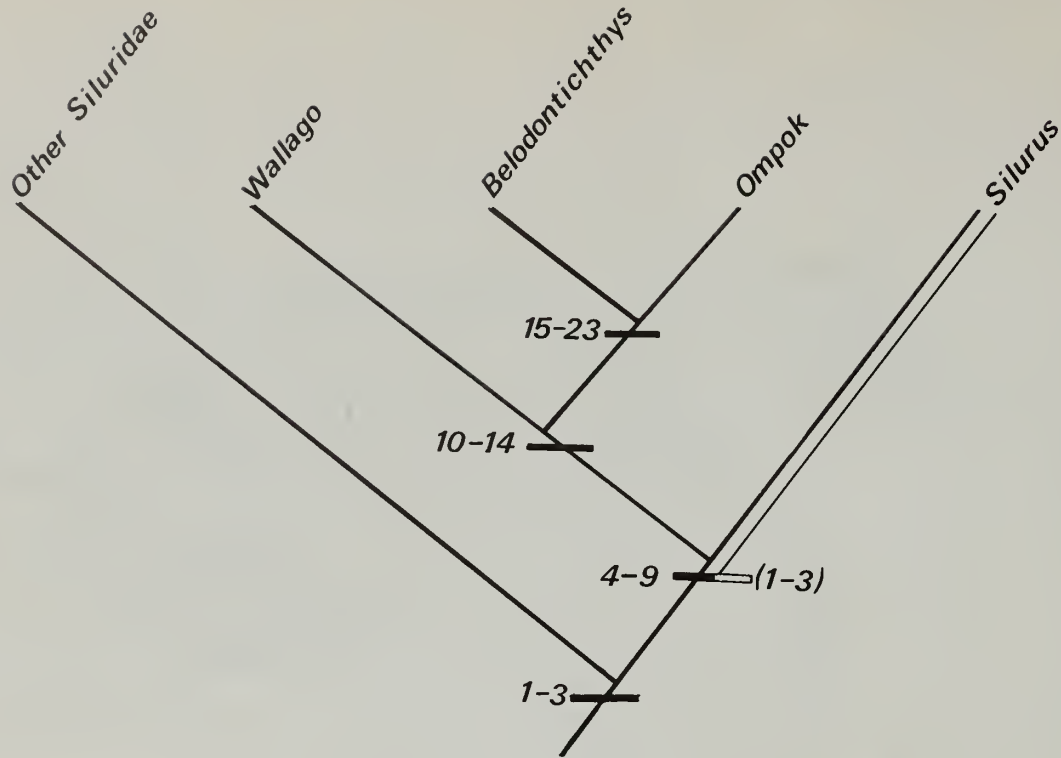
Fig. 27 Cladogram of Siluridae constructed from the synapomorphies discussed in the text (p. 00). Monophyly of the Siluridae follows Bornbusch (1990) with the addition of three other synapomorphies (1–3) involving frontal sensory canals, hyomandibular crest and *extensor tenatculi* muscle (p. 00). Characters 1–3 are absent in *Silurus* (see Discussion). The 'other Siluridae' lineage comprises *Hemisilurus, Ceratoglanis, Kryptopterus, Silurichthys* and *Ompok sensu lato* (see text).

infraorbital sensory canals. According to Lundberg (1982) the anterior displacement of the temporal canal branching point into the frontal is the result of jaw muscle insertion on to the cranium. In the Siluridae the development of the lateral branch of the frontal canal was also possibly initiated by encroachment of muscle onto the cranium, in this case, however, epaxial rather than jaw adductor muscle.

The sequence of phylogenetic changes culminating in the derived condition of the *Belodontichthys* cranium are evident in the successively derived sister-taxa *Wallago* and *Ompok* in which the lateral branch of the frontal sensory canal occurs transversely in the former and backwardly curved in the latter, with correlated anterior shifts of the cross-commissure, truncation of the anterior fontanel and posterior lengthening of the frontal crest. Concomitant with these changes in frontal topography is the forward encroachment with epaxial musculature on to the bone. In no other teleost known to us has the forward extension of the epaxial musculature produced such a profound modification to the frontals.

Among otophysans only two cyprinids *Macrochirichthys* and *Pelecus* display similar modifications. In both these taxa the frontals are concave but principally in the transverse and only slightly in the axial plane; in neither is there a median frontal crest. In both taxa the epaxial muscle extends to the anterior margin of the frontal, as in *Belodontichthys*. *Macrochirichthys* has anterior vertebral modifications which enable it to elevate the cranium, apparently to a considerable angle (Howes, 1979). Likewise, judging from the shape of the first centrum *Pelecus* may also have the ability to elevate the skull acutely. In the only other otophysans which have the capacity for marked cranial elevation (cynodontine characoids) the epaxialis musculature extends forward to the fronto-parietal ridge but the bulk of the muscle inserts into the posttemporal fossae (Howes, 1976). Cranial elevation in these fishes relies on the constriction of thick, longitudinal

tendons fixed to the pterotic (Lesiuk & Lindsay, 1978). In these taxa and *Macrochirichthys* the epaxial musculature has a complex layering, with a lateral cage of intermuscular bones which prevents lateral distortion of the epaxialis when the head is flexed; furthermore, a highly-developed *supracarinales anterior* muscle is present (Howes, 1976; 1979).

None of these features is present in *Belodontichthys* and the firm attachment of the posttemporal to the pectoral girdle suggests that the forward extension of the epaxial musculature functions as a head-restraining rather than as a head-raising device. Bornbusch (1988) has pointed out that the posttemporal articulates with the 4th vertebral transverse process *via* a ball and socket joint which possibly allows cranial elevation. While we do not rule out the possibility of some degree of cranial elevation the firm union of the 1st centrum with the complex vertebrae suggest that the cranium is more or less fixed at an oblique angle, the degree of which is further enhanced by the even more acute upward angles of the parasphenoid and the ethmoverine block (p. 138). In this way a stable structure is formed against which the lower jaw can exert a powerful bite. In this respect the cranium of *Belodontichthys* more closely resembles that of the osteo-glossomorph *Osteoglossum* (and to a lesser extent, *Scleropages*) which also has obliquely angled jaws and cranium, with an acutely angled parasphenoid, that promote powerful biting forces. In these fishes, however, the biting surfaces are principally between the toothed parasphenoid and basibranchial (Sanford & Lauder, 1990). Within siluroids, the closest functional equivalent appears to be the schilbeid, *Eutropiichthys vacha* which has paralleled the osteoglossoid 'tongue-bite' mechanism through the acquisition of extensively toothed vomerine and pterygoid toothed surfaces against which an inferior lower jaw bites. *Belodontichthys* lacks the vomerine and pterygoid development of *Eutropiichthys* and its lower jaw extends forward beyond the
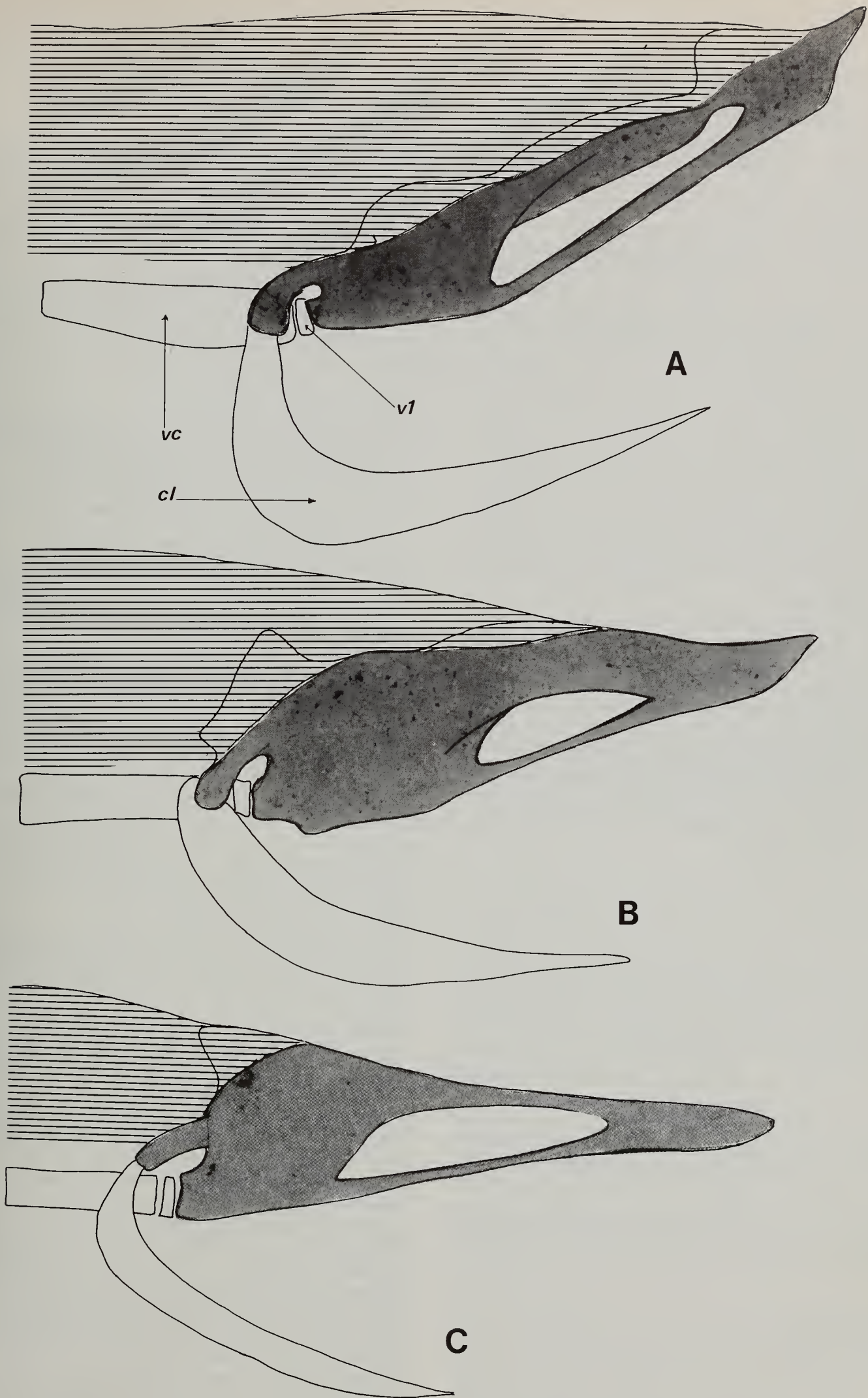
Fig. 28 Orientation of the cranium (shaded) with respect to the vertebral column, the pectoral girdle and extent to which the muscle has extended anteriorly (horizontal lines) in A, *Belodontichthys dinema*: B, *Ompok bimaculatus;* C, *Kryptopterus bleekeri*. The dorsal outline of the frontal-supraoccipital crests is indicated beneath the epaxial musculature. Drawn from radiographs.

upper so that only the long inner row dentary teeth bite against the outer row of premaxillary teeth (Figs 1B, C).

The head and jaws of juvenile *Belodontichthys* appear much as in *Wallago* but during development the jaws become obliquely aligned (C. Vidthayanon pers. comm.). Whether the epaxial muscle continues to extend forward onto the cranium during early development is unknown.

A low coronoid process of the lower jaw is a feature common to all those teleosts with long jaws having a snapping action, as are long caniniform teeth arranged in single or double rows. The latter feature is rare in siluroids, where the characteristic dentition is short, multi-rowed, villiform teeth. The only other siluroid to have a single row of large caniniform teeth is the sisorid, *Bagarius*, a large predatory fish with a widespread distribution in India and south east Asia (Roberts, 1983).

Belodontichthys falls into the category of teleosts which Ganguly & Chatterjee (1963) referred to as 'bilaterally compressed snapping teleosts' and in which they included *Ompok* and *Eutropiichthys*. *Belodontichthys* displays a morphotype which at first sight one might label as typically that of a 'neck-bending' teleost but closer examination reveals that this 'typical' morphology in fact characterises the converse functional situation, namely one providing a rigid rather than a flexible framework, presumably allowing more powerful biting forces.

We believe that the specialized features of the *Belodontichthys* cranium have arisen as a result of coordinated factors comprising cranial re-alignment with respect to the vertebral axis and the encroachment of epaxial muscle onto its surface (Fig. 28). The epaxial muscle encroachment has also resulted in the differential growth of the central areas of the frontal relative to its lateral areas thus maintaining the fixed position of the sensory canal pores around the perimeter of the muscle bloc. The jaw teeth have elongated and the dentigerous area has been reduced but the characteristic silurid prognathous lower jaw has been retained.

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